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SOME PHYSIOLOGICAL EFFECTS OF RADIUM RAYS[1]

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IT is probable that no scientific discovery, since the publication of Darwin's "Origin," has so revolutionized our conceptions of natural phenomena as has the discovery of radioactivity by Henri Becquerel, and of radium, by M. and Mme. Curie and Bémont. In the light of these epoch-making discoveries we have completely revised our concepts of the nature of matter and of electricity. The atom, the "undivided," has been shattered into fragments, and a large percentage of the investigations in the realm of physics and chemistry now have to do with atomic disintegration and the behavior of the resulting products.

It was Rutherford and Soddy who first proposed the hypothesis that radioactivity is a manifestation of the disintegration of atoms, and this hypothesis, chiefly through the investigations of Rutherford, has already assumed the rank of a theory.

It would be superfluous to enter here into a detailed account of the nature of radioactivity, as understood at present. Suffice it to say that the theory elaborated by

[1] The investigations embodied in this paper are treated more fully in the author's memoir on "Effects of the Rays of Radium on Plants" (*Mem. N. Y. Bot. Garden*, 4. Sept., 1908). It has not been thought desirable to enter into a discussion here of previous researches on the subject, since the literature is fully treated in the memoir. It is a pleasure again to express my indebtedness to Mr. Hugo Lieber, of Lieber & Co., New York City, whose great liberality in supplying all the radium made the investigation possible.

Rutherford involves a conception of the atom as a body composed of intricately related units. These units possess relatively enormous amounts of kinetic energy, and are in rapid orbital motion within the atom. In some substances of high atomic weight, such as uranium, polonium and radium, these units spontaneously escape from the atom and fly off into space. Such substances are called radioactive, and the emission of these units is radioactivity.

The particles themselves are called ions. They are of at least two kinds; one, called the β particles, very small (about one one-thousandth the size of a hydrogen atom), bearing a charge of negative electricity, and moving with a velocity approaching that of light; the other called α particles, about twice the size of a hydrogen atom, bearing a positive electrical charge, and moving at a much lower velocity than the β particles. The β particles or negative ions are called electrons.

Streams of negative electrons constitute the so-called β rays; streams of positive ions the α rays. Both α and β particles move with velocities that vary between certain limits and so the respective rays are complex.

In addition to the giving off of α and β rays, radioactivity involves the emission of electro-magnetic pulses in the ether. These are analogous to very penetrating X rays, and are called γ rays.[2]

The enormous velocity of the β particles, combined with their inconceivably small size, renders them very penetrating. They pass readily through matter opaque to light, moving between the molecules, or even passing directly through the latter, being smaller than the spaces by which the atoms are separated within the molecule. In their passage through substances they may collide with and so dislodge other electrons, thus producing ionization. The α particles, owing to their larger size

[2] Jean Becquerel (*Compt. Rend. Acad. Sci. Paris*, **146**: 1308. 22 Je 1908, **147**: 121. 13 Jl, 1908) reports the experimental demonstration of the existence of free *positive* electrons, but whether such electrons are involved in radioactivity has not been determined.

and lower velocity, are less penetrating than the β particles, but are much more effective ionizers. The γ rays behave as X rays.

In addition to the three types of rays above described, radioactive substances are the source of a heavy, inert gas, belonging to the argon family. This gas, named by Rutherford the emanation,[3] is itself radioactive, giving off only α rays.

Studies of the physiological effects of radium, therefore, must take into consideration the three types of rays, described above, and also the radioactive gas, the emanation. In the experiments recorded below, the radium, in the form of radium bromide, was contained in sealed glass tubes, or employed as a thin coating on a suitable surface. In the former case only X and γ rays were available, as the α rays and the emanation can not pass through the walls of the tubes. In the latter case the α rays together with the emanation were also available.

The effects of radium upon plants have been investigated by Dixon and Wigham[4] in Great Britain, by Koernicke[5] in Germany, by Guilleminot[6] in France, and by several others. Without going into the details of their work it may be stated that the general conclusion from their experiments is that the rays exert either a retarding or an inhibiting effect on physiological processes. Koernicke, however, found some evidence that acceleration of activity might follow exposure to the rays under suitable conditions.

My own investigations have led to the conviction, already reported,[7] that radium rays act as a stimulus to

[3] The use of the plural "emanations" to designate all the rays and influences coming from radium, has been somewhat common in biological papers. It has no warrant, is only confusing, and should be abandoned.

[4] *Nature*, **69**: 81. 1903. *Proc. Roy. Dublin Soc. Sci.*, N. S., 10^2: 178. 1904. *Notes Bot. School, Trinity Coll.*, Dublin, **1**: 225. 1905.

[5] *Ber. Deut. Bot. Ges.*, **22**: 148, 155. 1904; **23**: 324, 404. 1905.

[6] *Compt. Rend. Acad. Sci. Paris*, **145**: 711. 1907; *Compt. Rend. Assoc. Française Adv. Sci.*, 36^1: 389. 1907; 36^2: 1344. 1908; *Compt. Rend. Acad. Sci. Paris*, **145**: 798. 1907.

[7] "Effects of the Rays of Radium on Plants." New York, 1908. (*Mem. N. Y. Bot. Garden*, Vol. IV.)

plants. If this stimulus ranges between a minimum and an optimum point an excitation of function results; if beyond the optimum point a depression of function, passing to complete inhibition as the strength or duration of the treatment is increased beyond the point of optimum stimulation. The following experiments are chosen from nearly 200, and indicate the nature of the evidence upon which the above conclusions are based.

Eight dry seeds of the bean (Phaseolus—Henderson's "Long Yellow, Six Weeks") were placed in moist sphagnum with their hilum-edges touching a rod coated with a Lieber's radium-coating[8] of 10,000 activity.[9] After

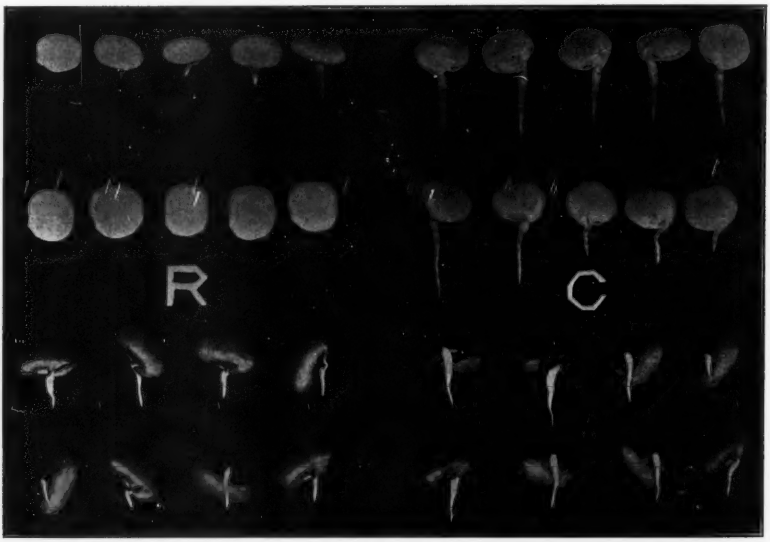

FIG. 1. Effect of radium rays on the germination of *Lupinus albus* and *Phascolus*.

three days (70 hours) exposure, the radicles of the exposed seeds averaged 13.18 mm. in length, those of a control set 15.12 mm. Ten dry seeds of *Lupinus albus* were similarly exposed to a coated rod of 25,000 activity and,

[8] See Gager, *l. c.*, Chapt. VI.

[9] The unit of activity is the activity of uranium. Radium of, *e. g.*, 10,000 activity is 10,000 times as active as uranium.

at the end of three days (70 hours) the radicles of the exposed seeds averaged 3.81 mm. in length, those of the control set 21.80 mm. The retardation of germination and growth following this treatment is illustrated in Fig. 1.

A row of timothy grass seed (*Phleum pratense*) was sown on a moist blotter. Over the center of the row was suspended vertically a sealed glass tube containing 10 mg. of radium of 1,500,000 activity in the end of the tube nearest the seeds. The distance from the tube to the seeds was about 5 mm. A second row was also arranged as a control (not exposed to radium). At the end of eleven days the control seedlings were all of about the same height and color (normally green) and averaged 30 mm. in height. The exposed plants were entirely etiolated directly under the radium tube and for a radius of 4 mm. on each side. The height of the seedlings gradually decreased from 30 mm. (average) at the

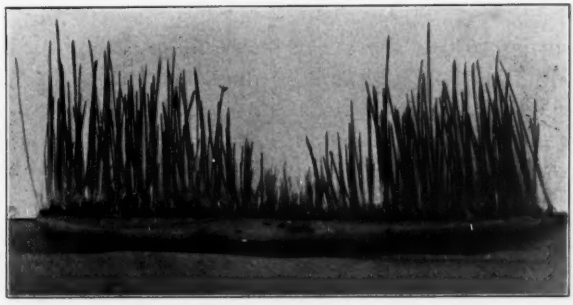

FIG. 2. Effect of radium rays on the germination and growth of timothy grass.

ends of the row, to 3 mm. at the center under the radium (Fig. 2).

Twenty seeds of "Lincoln" oats (Avena), with the glumes removed, were placed in two parallel rows with the radicle ends touching, and the embryo-side uppermost. Over them was laid the sealed glass tube of radium bromide of 1,500,000 activity, resting on the radicle ends of the seeds. After an exposure of 6 days

and 15 hours, these grains, together with twenty similar but unexposed ones, were planted in flower pots in soil. The control grains germinated two days sooner than those exposed, and, at the end of seven days after planting, the seedlings from the exposed grains were just appearing above the soil, while the control plants were several centimeters tall (Fig. 3).

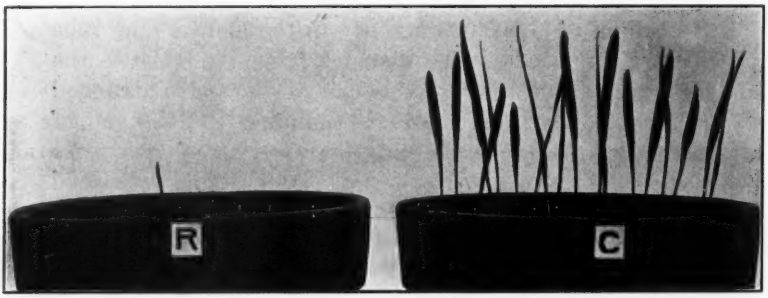

FIG. 3. Effect on the germination and growth of oats of exposing the grains before planting. Cf. Fig. 4.

In order to test the effect on germination and growth of radium rays in the soil, 16 unsoaked grains of "Lincoln" oats were sown in soil in a flower pot, in 3 concentric circles, at distances of 7 mm., 22 mm. and 45 mm. from the center of the pot. At the center

FIG. 4. Acceleration of germination and growth of oats by placing a sealed glass tube of radium in the soil (R). The tube in C is empty. Cf. Figs. 3 and 5.

the sealed glass tube of radium (1,500,000 ×) was inserted vertically into the soil, with the end containing the radium at a depth of about 5 mm. below the surface. A control culture was similarly arranged with an *empty* glass tube. After an exposure of 106 hours the seedlings in the pot containing the radium were all up, and were most decidedly taller than those in the control culture, three of which were not yet up, and all of which were less developed in every way than those exposed to the radium.

The plants in the outer circle of the exposed culture averaged 50 mm., those in the middle circle 46 mm. and those in the inner circle 42 mm. taller than those in the corresponding circles of the control (Fig. 4).

On the sixth day after planting the radium tube was changed to the control culture, and the empty tube replaced the radium. The pot C was then irradiated (CR)

FIG. 5. The same cultures as those shown in Fig. 4, six days later. The radium tube is now in C (CR), and R serves as the control. Cf. Fig. 4.

and R became the control. At the end of five days after this change the plants in CR (Fig. 5) were nearly as tall as those in C and the exposure was photographed. Eventually the plants in CR exceeded those in R, and thus, by changing the radium tube from one pot to the other, the growth of either culture could be accelerated at will.

In order to ascertain the effect on growth of exposing seeds for the same length of time to radium of various degrees of activity, three sets, A, B and C of six dry seeds each of *Lupinus albus* were exposed to rays from radium in sealed glass tubes by laying the tubes against the hilum-edges of the seeds. The duration of exposure was 91.5 hours, and the strengths of the radium as follows: A, 1,800,000 ×; B, 1,500,000 ×; C, 10,000 ×; D, control, not exposed. At the close of the period of exposure the seeds were planted in soil, each set in a different pot. The experiment was photographed eleven days after the seeds were planted (Fig. 6), and curves of growth of the

FIG. 6. Effect on growth of exposing seeds of *Lupinus albus* for 91.5 hours to rays from radium of various degrees of activity. From left to right the activity was 1,800,000; 1,500,000; 10,000; C, control. Cf. Fig. 7.

four cultures are shown in Fig. 7. It is seen at a glance that the effect of the rays on growth varies directly with the degree of activity of the radium. The apparently anomalous rise of the 1,800,000 curve during the first days record (Fig. 7) is due either to poor exposure of some one of the seeds of that culture, or represents an individual variation in resistance to the rays that was not compensated for because of the small number of seeds necessarily employed.[10]

To show the effect of duration of exposure to radium of the same activity, four sets of six dry seeds each of *L. albus* were taken. Three of them A, B and C, were exposed as follows to the rays from 10 mg. of radium

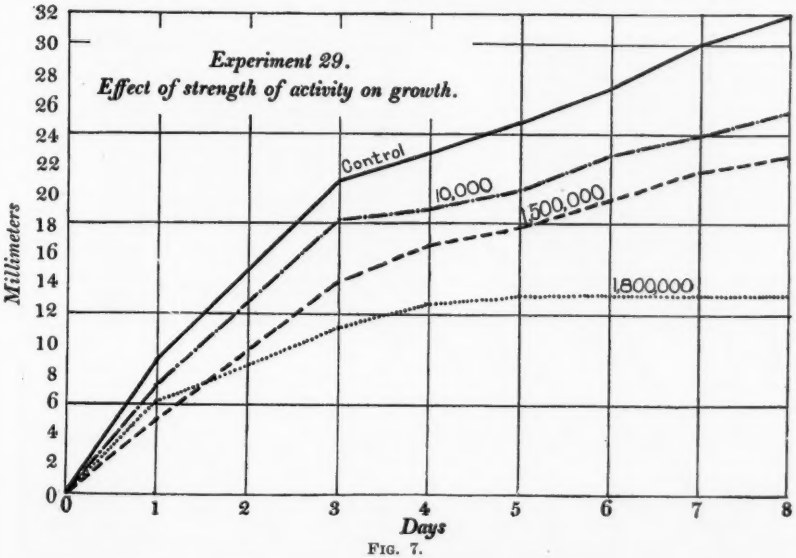

FIG. 7.

bromide of 1,800,000 activity, in a sealed glass tube: A, 72 hrs.; B, 50 hrs.; C, 26 hrs.; D, control, not exposed. The seeds were then planted, without soaking, in separate pots of soil. At the end of 5 days the average heights of the seedlings above the surface of the soil were as follows: A, 88 mm.; B, 95 mm.; C, 134.50 mm.; D, 145 mm. Inspection of the curves of growth for the four cultures (Fig. 8) shows that, for a given activity of radium, the effect on growth varies directly with the duration of the exposure.

The retardation of starch formation by a green leaf in the light was shown as follows. A nasturtium (*Tropæolum*) plant was removed to the light after being in darkness for 18 hours. Under one of the leaves,

[10] The length of the tube did not permit of satisfactorily exposing a larger number of seeds at one time.

empty of starch, was placed a Lieber's radium-coated rod of about 25,000 activity. The rod was placed under the leaf in order not to shade the latter. After an exposure of twenty-four hours the leaf was decolorized and tested with iodine. Abundant starch was found on the edge of the leaf farthest from the rod, but only very slight

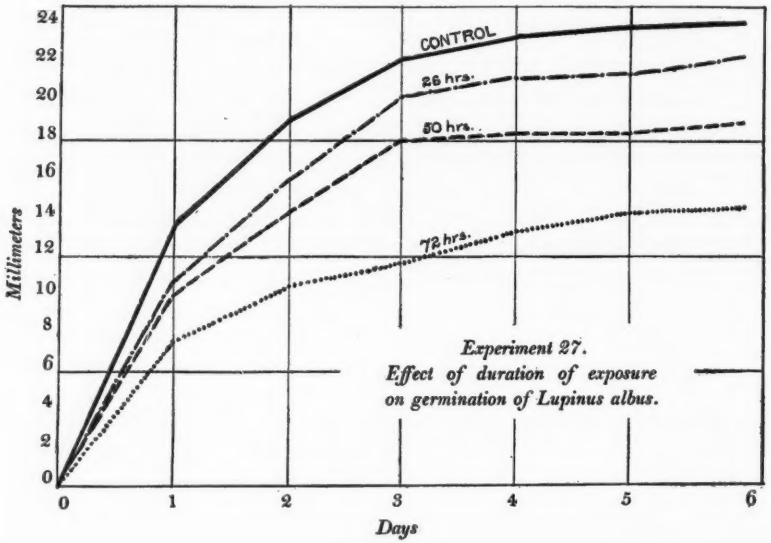

FIG. 8.

traces elsewhere, especially in the region that was directly over the rod. A print of the leaf was made by laying it over a sheet of velox paper in a printing frame and exposing it to light. In this way the portions having less starch, and, therefore, more transparent, showed darkest on the print (Fig. 9).

All attempts to demonstrate a direct tropistic response to the rays, by either roots or shoots, were unsuccessful. When, however, a sealed glass tube containing about 50 mg. of radium bromide of 10,000 activity was suspended horizontally in a culture solution, at a distance of from 2–10 mm. from the root-tips of *L. albus,* the roots curved toward the tube (Fig. 10). In an experiment in which

a culture solution was substituted for the tap-water, the angle of curvature was more abrupt (nearly 90°). It seems probable that this is an indirect response, due to the effect of the radium rays on the water or solution.

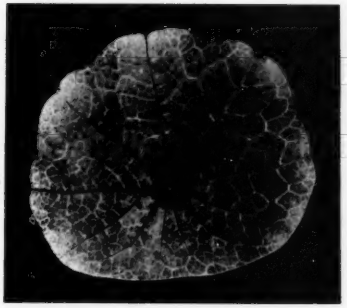

FIG. 9. Retardation of photosynthesis by radium rays. A direct heliograph, made by interposing the leaf between velox paper and the light. The darker portion represents the region exposed to the rays.

FIG. 10. Curvature of root-tips toward a sealed glass tube of radium bromide (10,000×) in a culture solution.

Whether the rays increase the number of ions of an electrolyte in solution is still a debated question,[11] but the physiological effects of tap-water exposed to the rays seem to leave no doubt but that the latter alter a solution in some way. How, we do not know.

Micheels and de Heen[12] were among the first to study the effect of the rays on plant respiration. Under the conditions of their experiments respiration was always retarded. In one of my own experiments, soaked grains of wheat (*Triticum*) weighing, when dry, 2 gm., were supported on a moist blotter in a tumbler over a saturated solution of KOH. Over the wheat, and in contact with the grains, was placed the sealed glass tube of radium of 1,500,000 activity. The CO_2 given off by the wheat was absorbed by the KOH, and the consequent rise of mercury in a graduated tube of small bore was taken as an index

[11] Cf. *Mem. N. Y. Bot. Garden*, **4**: Chapt. XIX. 1908.

[12] *Bull. Acad. Roy. de Belgique Class. Sci.*, p. 29. 1905. *Bot. Cent.*, **98**: 646. 1905.

of the rate of respiration. Under such conditions, and with radium of 10,000 as well as 1,500,000 activity, the result was always an acceleration of respiration, as is shown in Fig. 11. It is probable that, under certain con-

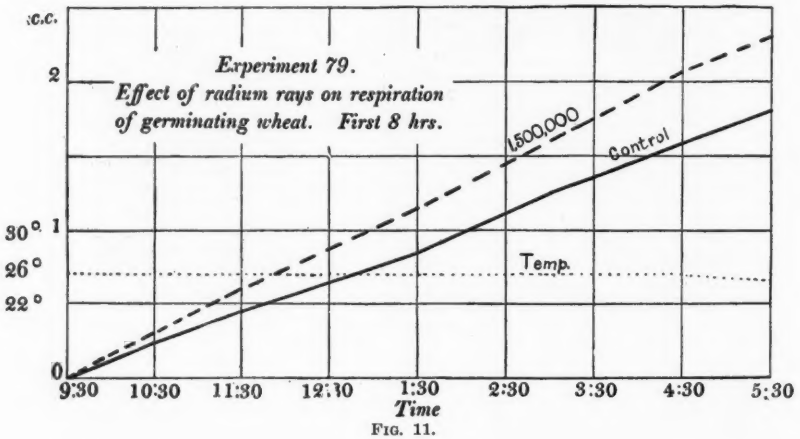

FIG. 11.

ditions of exposure, the rays would retard or completely inhibit respiration.

In order to test the influence of the rays on alcoholic fermentation, mixtures of commercial yeast in ferementation tubes were exposed to the rays. A piece of compressed yeast weighing 1 gm. was thoroughly mixed in 100 c.c. of tap-water, and equal portions of this mixture were placed in fermentation tubes. Into these tubes were placed sealed glass tubes containing radium bromide of activities 7,000, 10,000 and 1,500,000. A fourth fermentation tube with no radium served as a control. The rate of fermentation was measured by the rate of evolution of the gas. The results of all experiments indicated a decided acceleration of fermentation under the influence of the rays, and, as the curves in Fig. 12 clearly show, the amount of acceleration is in direct proportion to the activity of the radium.

No reference has yet been made of the fact that radioactivity is a factor in the normal environment of plants.

I have elsewhere[13] noted this, and have presented[14] a mass of evidence from the realm of physical science indicating the general distribution of radioactivity. It exists in air and soil, in spring-water, and in freshly fallen rain and snow. Potassium, one of the essential elements of

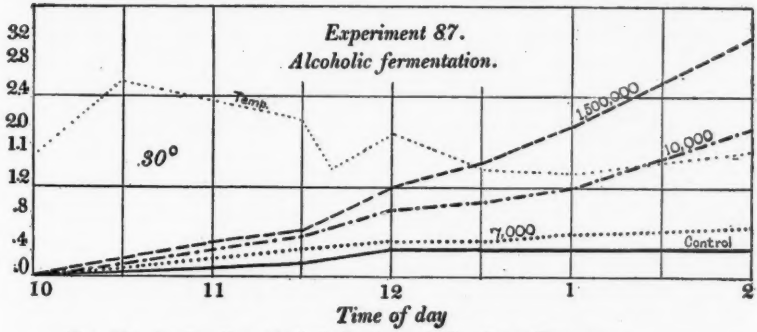

FIG. 12. Acceleration of alcoholic fermentation by radium rays.

plant food, has been found by Campbell to give off β rays,[15] and some evidence has also been found that calcium possesses the same property. The researches of many investigators have clearly demonstrated the general occurrence in nature of free negative electrons. These discoveries not only add to the interest and importance of the study of the physiological rôle of radium rays, but also point out the way for further investigation.

An arrangement devised by Mr. Hugo Lieber facilitated the study of the effect of a radioactive atmosphere on germination and growth. The apparatus is clearly shown in Fig. 13, and needs little further explanation, except to say that the hollow cylinder, R, has its inner surface coated with a Lieber's radium coating. The bell-jars fit tightly on to the ground glass plates, and a current of air is kept passing through the jars by attaching the tubing from the lower tubulure to an exhaust pump. The air passing through the radium-lined cylinder carried with it the emanation given off by the

[13] *Science*, N. S., **25**: 263. 1907.

[14] *Mem. N. Y. Bot. Garden*, **4**: Chap. II. 1908.

[15] *Proc. Cambridge Phil. Soc.*, **14**: 211. 1907. *Nature*, **76**: 166. 1907.

radium, and thus the plants were subjected chiefly to the influence of α rays.

In the experiment here described, dry seeds of timothy grass were sown on the surface of the soil in two pots

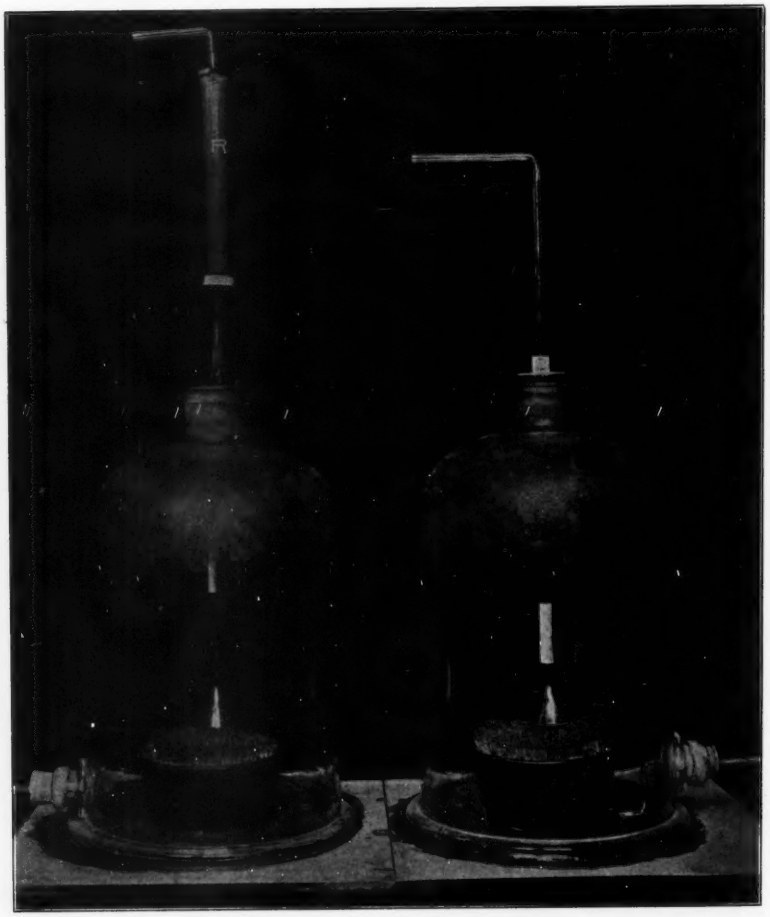

FIG. 13. Apparatus for growing seedlings in a radioactive atmosphere. Cf. Fig. 14.

and placed, one under each of the bell-jars. After five days, during which a continuous current of air was de-

livered over the cultures, the seeds were found to have germinated and grown uniformly under the control jar, but, in the culture exposed to the emanation, the seeds immediately under the funnel through which the emanation was delivered had entirely failed to germinate. The other seedlings of this culture were only very slightly less vigorous than those of the control (Fig. 14).

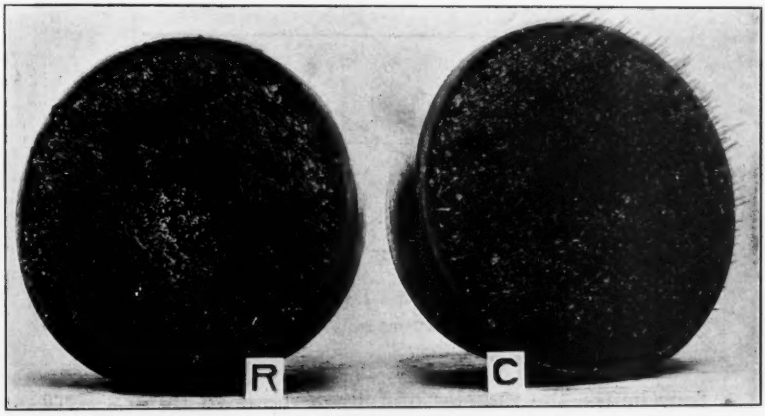

FIG. 14. Result of growing timothy grass in a radioactive atmosphere as shown in Fig. 13, R, exposed cultures; C, control.

To further investigate the effects of this radioactive air, five germinated seeds of *L. albus* with radicles over 10 mm. long were marked with India ink 10 mm. back from the root-tip. These seedlings were then suspended vertically, five under each bell-jar. The air, normal in one jar, radioactive in the other, was forced into the bell-jars by means of a rubber bulb, the blasts being given at irregular intervals of from two to twenty-four hours. At the end of the first twenty-four hours the average length of the exposed radicles was 19.00 mm., and of the control only 12.10 mm. At the end of the second twenty-four hours the average lengths were, for those exposed 23.30 mm., for those unexposed, 12.70 mm. The curves of growth for this experiment are given in Fig. 15, showing the acceleration in rate of growth under the conditions imposed.

The growth of roots was retarded in water exposed for twenty-four hours to the rays. The experiment was made as follows: Into 100 c.c. of tap-water, in which sealed glass tubes of radium bromide had lain for twenty-

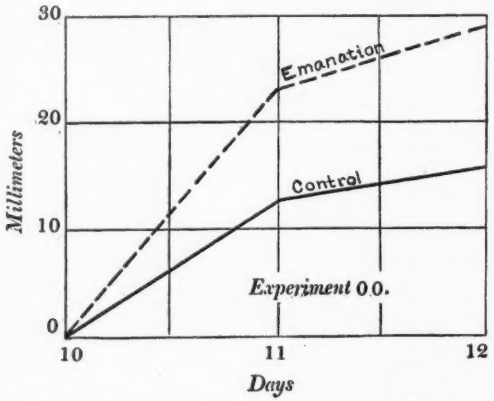

FIG. 15. Acceleration of growth of roots of *Lupinus albus* in a radioactive atmosphere.

four hours, the radicles of four germinated lupines were suspended up to an ink mark, placed 10 mm. back from the root-tip. Three cultures were arranged: A, with radium of 1,800,000 activity; B, with radium of 1,500,000 activity; and C, with no radium, serving as a control. At the end of five days the average lengths of the hypocotyls were, for A, 79.62 mm.; for B, 85.50 mm.; for C, 117.75 mm. The result, then, was a retardation of growth, in direct proportion to the degree of activity of the radium to which the water was exposed (Fig. 16).

Following up the suggestion in the discovery that freshly fallen rain is radioactive, several experiments were made with a view of ascertaining the effect of this radioactivity on plant growth. Rain-water was caught in the open, in chemically clean glass dishes, after about four hours of rain, so that the air was well washed. This water was kept carefully covered, for one month, when another opportunity presented itself of collecting another lot of rain under similar favorable circumstances. The

experiment was set up immediately after the last collection, using radicles of *Lupinus albus*, immersed to a measured length of 5 mm. in both the fresh and the stale water. Two parallel experiments, A and B, were run,

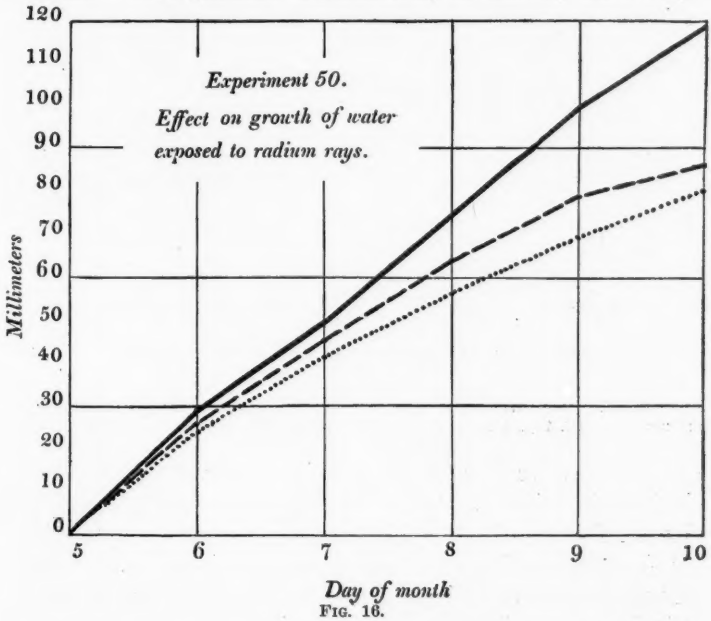

FIG. 16.

each with a "fresh" and a "stale" culture. At the end of 48 hours the lengths of the radicles averaged, for set A, 23.50 mm. fresh; 27.50 mm. stale: for set B, 22.38 mm. fresh; 27.00 mm. stale. The curves of growth are shown in Fig. 17. The experiments of which this is a type indicate that, as a result of its radioactivity, freshly fallen rain water tends to retard the growth of roots. We have as yet no data on the effect of this factor on the activities of the shoot.

Profound histological changes follow exposure to the rays. These effects are due chiefly to a disturbance of the normal functioning of the cambium, and are in harmony with results of experiments on animals, in which it has been shown that embryonic tissue is more sensitive

than any other. After an exposure of seeds under certain conditions, the cambium is frequently entirely lacking, all of the cells in the given organ having passed over into the mature state. The treatment appears to accelerate the approach of senescence.

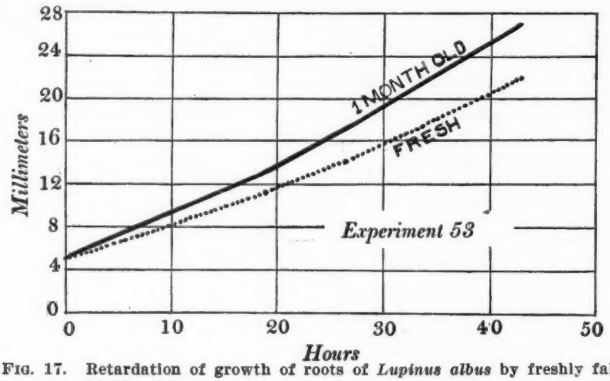

FIG. 17. Retardation of growth of roots of *Lupinus albus* by freshly fallen rain water. Cf. Fig. 16.

Exposure to the rays also induces marked irregularities in mitosis. This is shown, among other ways, by the failure of some of the chromosomes to take part in the organization of the daughter nuclei. Usually such chromosomes organize smaller, nuclear-like structures within the daughter-cells. In one instance they were observed to be undergoing an independent karyokinesis at one side of the main mitotic figure. Interesting possibilities are here suggested, along the line of experimental mutation.

Experiments like those described in this paper have been many times repeated with confirmatory results, and seem amply to justify the general conclusion, earlier stated, that radium rays are a stimulus to plant activities. The reaction to a stimulus between the minimum and optimum points is an excitation, or acceleration of the given process; the reaction to an over (superoptimal) stimulus is a depression, or retardation of function, and, if the stimulus is sufficiently intense, complete inhibition or ultimate death.

ON THE ORIGIN OF STRUCTURES IN PLANTS

W. A. CANNON

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THE systems of organs of which a higher plant more especially is composed generally hold an intimate physical relation to one another. They are bound together so intimately by reason of their position in root or shoot that the growth, development or response to stimulus of one is in a very great measure molded by the growth, development or reaction of all the rest. In addition to these considerations, when the origin of tissues or of organs is being investigated, account must also be taken of the nutrition of the special organ as well as its especial relation to environment external to the plant of which it is an integral part. Thus the complex physical interrelations, and the physiological correlations as well, make the study of the functions, and behavior of the individual tissue, or organ, as a possible independent unit one of great difficulty. These general facts probably hold for plant tissues as a whole, but one system, namely, the trichomal system, offers a favorable field in which to study the origin, development and biological relationships of plant organs, inasmuch as it is comparatively little affected by other tissue systems. Beyond growing out of epidermal cells, remaining permanently attached to the epidermis, and deriving nourishment from the subjacent cells, the trichomes lead an independent existence, and in origin, development and form are not directly influenced, as the other tissues are affected, by the pressure of enveloping tissues, and in certain plants, as *Franseria dumosa,* the trichomes go one step further on the road to independence, in that they are chlorophyll-bearing and in a sense probably auto-trophic. For these and other

reasons the trichomes are favorable for the study of the origin of plant structures, as I recently found while working on certain hybrids, a detailed account of the results of which will be given in another place.

The walnuts, to which reference is made, bear 4 or 5 types of multicellular hairs, besides certain abnormal and one aberrant type. These are composed of 6, or 8 cells, or about 16 or about 32 cells. A close study of the development of the trichomes, in which mitotic figures were used as indicators of the course of cell division, showed the following to be facts: (1) In the earliest stages of development of all of the normal trichomes, the sequence of the first two, or three cell divisions was the same; (2), the sequence of cell divisions of the 6-celled and the 8-celled trichomes, during the entire development, is consistent; (3), the 8-celled trichome recapitulates faithfully the sequence of cell divisions of the 6-celled type up to the six-celled stage, and then adds two divisions in an order not departed from. Certain facts indicated that the late cell divisions of the two larger forms of trichomes, namely, those with about 16 and about 32 cells, do not hold to a sequence so closely, but further study of these difficult trichomes might modify this conclusion. These facts indicate that all of the multicellular trichomes may have originated in a common ancestral form and that by

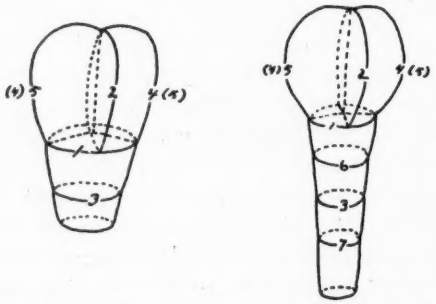

FIG. 1. Semi-diagrammatic sketches of 6- and 8-celled trichomes to show the Cell Lineage of each. The numbers refer to the sequence of the formation of the cell walls.

arrested development, or other differentiation, the various types of trichomes now to be found in Juglan's species have arisen. Certain of the trichomes are evidently more closely related to one another than to other types, and thus the trichomes are not all of equal age, but have been derived from an ancestral form at various times in the history of the plants which bear them. It is very probable, for instance, that the 6-celled type is more nearly related to the 8-celled type of trichome, than it is to either of the larger forms, but it would be difficult to say which represents the more ancient type. In development, and probably in origin, the types of trichomes thus behave as if they were separate organisms, or independent units of a complex organism. This is not the same as saying that each type of trichome is a "unit character," although certain observations which I have made on the distribution of trichomes in another plant, as well as the reversion of the trichomes in the second generation of *Juglans californica* × *Juglans regia* would justify this conclusion. Should it be the experience of other observers also that each type of trichome has its peculiar area of distribution in a plant, the conclusion that each form of trichome represents a separate unit character could not be avoided, and from such structural studies as above reported we should be able to trace their very origin as separate portions of the tissue of the plant.

In addition to the normal types of hairs in walnuts, as given above, there are also other types. Of such, there are certain abnormal forms which are evidently related to the already existing trichomes, of which they are slight modifications, and one aberrant type which is essentially different from these. The origin of the aberrant form was seen also, and was found to be as different from the mode of origin of the normal trichomes as the mature aberrant type is different from the mature normal form. In brief, its departure from the normal takes inception in the orientation of the first cell wall, which is longitudinal in place of being transverse as is usually the case (Fig.

2). Consequently it happens from this single initial deviation, there arises a form of trichome, unrelated to other existing types, and, consequently, of which it can in no wise be said to be a modification. In fact the new hair is a mutation, and its history shows in at least one way how such variation has its origin. In this instance there is no disappearance of intermediate forms of trichomes, since for structural reasons there can not be such.

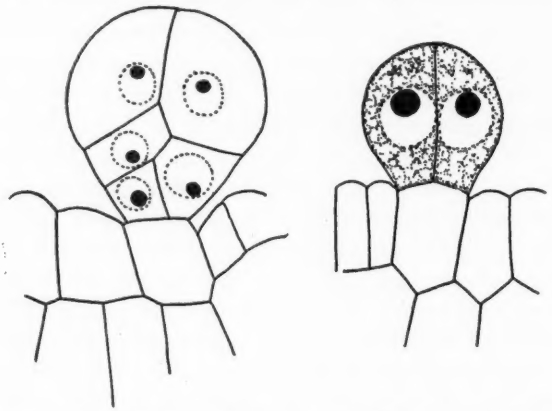

FIG. 2. Mature aberrant Trichome and two-celled aberrant Trichome, in which the first cell wall is laid down parallel to the long axis of the mature hair.

We therefore find in Juglans that the different types of multicellular trichomes may take their origin in one of two ways, namely, they may arise as modifications of types already existing in the plant, which is apparently the usual manner, or they may arise suddenly and hence provide points of departure for subsequent trichome formation and differentiation of which they would be the ancestral type.

The physiological reasons for the differentiation of the trichomes were not investigated, but observations indicate a close relation between size of hair and the position occupied by it on the plant member, and suggest that the factor of nutrition may be important in inducing certain, at least, of the irregularities noted.

THE ORIGIN AND FORMATION OF THE FROTH IN SPITTLE-INSECTS[1]

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DURING the summer months one observes upon trees, shrubs, herbs and grasses, numerous masses of froth-like material, which resemble large drops of spittle. An examination of a frothy mass soon discloses the presence of a small insect, greenish, brownish, or whitish in color, depending upon the species under observation. This is the immature nymphal stage of an insect belonging to the homopterous family Cercopidæ. So far as it is known, all the members of this family surround themselves with such a secretion, in which they spend their nymphal life. I have had under observation three species, *Aphrophora parallela* Say, *Lepyronia quadrangularis* Say, and *Clastoptera proteus* Fitch. Each of the species studied in this locality makes a characteristic froth, as may be easily recognized by a little study.

While there is much which has been written upon the production of froth by the insects of this group, the opinions of the many writers are very much at variance. This is especially true regarding the more recent literature on the subject. For this reason it seemed desirable to undertake a detailed study of this subject and to determine what organ or organs were concerned in the production of this secretion. This study consisted not only of field observations and laboratory experiments, but of a detailed study of the histological structures concerned.

This work was carried on in the Entomological Laboratory of Cornell University, and to its director, Professor J. H. Comstock, I am indebted for many courtesies. The problem was suggested by Dr. W. A. Riley, and to him I am indebted for constant aid and advice.

[1] Contribution from the Entomological Laboratory of Cornell University.

HISTORICAL

Gruner (1901) has given a very extended and excellent historical account of the work of individual writers on these insects. It is intended here merely to group the views held by the various writers, at the same time adding the opinions held by writers since the appearance of Gruner's paper.

As far as the writer has been able to determine from original sources, there are seven theories which have been advanced in explanation of the production of the froth. This does not take into account the belief of the southern negroes, who claim that the frothy masses are caused by horseflies, neither does it take into consideration the opinion formerly held by many, that it is the product of the stars, nor the view that it exudes from the ground.

Isidorus, who lived in the sixth century, is cited by Gruner as the first to write on this subject. He believed that the froth was the spittle of the cuckoo bird, and that from this secretion the cercopid spontaneously generated. Mouffet (1634) and other writers came to the same conclusion respecting the origin of the spittle and insect. Aldrovandi (1610), in his Ornithologia, strongly denies this assertion, but fails to enlighten the reader as to the true solution of the problem.

According to Gruner's account, Bock (1546) apparently believed that the froth was the product of plants and he gave a list of the plants producing it.

John Ray (1710) states that the spittle mass was caused by the insect found within the mass, and believed that it was expelled from the animal's beak. He was upheld in this view even in recent times by as prominent an authority as Uhler (1884). Fabre (1900) states that a clear fluid comes out of the beak and that to this fluid the insect injects air bubbles by grasping air with the last pair of lateral prolongations of the ninth abdominal segments.

Blankaart (1688) believed that the froth came out of the anal opening of the insect. In this view he is supported

by Poupart (1705), Frisch (1720), Geoffroy (1764), De-Geer (1773) and others. Morse (1900) modified this view somewhat in that he gives as his opinion that what comes out of the anus is a " clear somewhat viscid fluid " and that by means of appendages at the extreme tip of its abdomen the insect secured a moiety of air by grasping it, so to speak, and then instantly releasing it as a bubble into the fluid. Gruner (1900 and 1901) states that the fluid is exuded from the anus and passes under the body, flowing into a pocket-like space where it becomes impregnated with air which comes out of the stigmata located in the pocket.

Porta (1900 and 1901) believed that there were openings on the dorsum of Aphrophora which were connected with oval glands little distinct from the hypodermis. He describes them as arranged at the base of the excretory canal in numbers of five, six or even fewer, indistinctly separated from one another. To these glands he ascribed the function of producing the fluid. He also states that the bubbles are blown into the fluid by the method described by Morse.

Girault (1904) states that " during the process of secretion the fluid flows slowly from a point near the anal opening, and gathers between the legs, where, by their alternate agitation, it becomes mechanically mixed with air and forms cushions of air bubbles," and he further states "that the air is taken in at each up and down motion of the abdomen and that during this dipping process the ventral plates are in transverse motion like jaws, and that it is probable that the secretory glands are between them." From this we should infer that he thought that it came from special secretory glands and not from the anus.

Berlese (1907) believes that the froth is secreted by glands found upon the seventh and eighth abdominal segments, previously described by Batelli (1891).

In the following it is proposed to discuss the evidences bearing upon each of the current views presented above

and give in details the observations made to clear up the confusion.

METHODS

The methods used in the biological observations are given in the body of the text. I refer here only to those used for the examination of the histological structures.

In preparing the tissues of the spittle insects for histological examination various methods of fixing, killing and staining were used. The best results were obtained by killing in hot water and then transferring immediately into Fleming's strong solution for twenty-four hours. Tissues killed directly in hot Fleming's fluid, while giving satisfactory differentiation of organs like the testes, intestine and fat cells, gave poor results with the glands. Very good results were obtained by killing in hot Gilson's fluid.

Good serial sections of the nymphs were obtained by infiltrating in paraffine 54° C., while adults imbedded in 62° C. paraffine gave better sections. Sections were cut from three to ten microns.

Staining was done on the slide with iron hæmatoxylin or Delafield's. Whenever the latter was used the tissues were counter-stained in eosin.

In order to get satisfactory preparations of the glands in surface view the tissues were killed in hot Gilson's fluid and allowed to stand for one half hour after having been opened and the fat carefully removed. After washing in seventy per cent. alcohol and a few drops tincture of iodine, the specimens were stained in borax carmine for a few minutes, dehydrated, cleared and mounted in balsam. Great care must be observed in teasing the fat away from the glandular region, otherwise the cells will be disarranged.

PERSONAL OBSERVATIONS UPON THE PRODUCTION OF THE FROTH

I first studied the gross features of the froth formation in several specimens. A large specimen of *Aphrophora*

parallela was taken from the frothy mass and by means of a camel's hair brush was thoroughly freed from every particle of froth. The specimen was then placed upon a dry twig. It soon inserted its beak in the plant and gradually increased in size. It projected the tip of its abdomen extensively and then retracted it. This operation it repeated several times. Suddenly a small drop of a clear liquid appeared at the very tip of the abdomen, coming distinctly out of the anal opening. Observations made with a hand lens upon other parts of the body, especially in the region of the dorsum, failed to show any fluid whatever. The small drop was soon joined by another, and these in turn were followed by many others, the whole mass of fluid passing down on the ventral side of the body along the channel formed by the sternites and the prolongations of the pleurites (Figs. 1 and 6). Again, the fluid was noticed to be fairly oozing out of the anal opening. After a quantity had accumulated about the body of the insect, it was noticed that the last pair of legs, sometimes also the second pair, would reach out to the region of the seventh and eighth abdominal segments, then rub against the body and against one another as if in the process of mixing substances. After the fluid had been well mixed and the surface had been covered by it, it was next observed that the nymph moved the tip of the abdomen out of the liquid, opening up the pair of lateral appendages of the ninth abdominal somite, which immediately closed again. Then with a downward movement these parts were immersed in the liquid and the appendages, upon being opened, released a particle of air in the fluid. This operation was repeated many times, with the result that the insect was soon covered with air bubbles, which gave the characteristic covering a froth-like appearance. It was noticed that by changing the size of the air-grasping pocket, the insect is able to make bubbles of any size. For that reason, the bubbles in the smaller forms are always very much smaller than those of the larger spittle insects. It is partly this feature

which determines the above-noted characteristic appearance of the froth of the different species. The insect does not always wait until the body is completely covered with fluid before injecting the air into it.

In order to make sure that the larger portion of the fluid came only from the anus, the latter was closed by a plug of lens paper, which being capped with balsam, and then allowed to dry for a few moments, closed the anal opening perfectly. The insect, upon being placed on a twig, after locating a satisfactory place, soon pierced the plant with its beak and began feeding. It rapidly increased in size and became much distended and swollen. Although observed for over three hours not a single drop of fluid came out. In a specimen whose anal opening had not been carefully sealed a drop of liquid succeeded in coming out of the tip of the abdomen, on the side of the filter plug. Thus it was demonstrated, as any one who desires to repeat the operation may, that at least one of the constituents of the froth is emitted from the anal opening, and that the views of Mouffet, Porta, Berlese and Girault are not correct, for according to their interpretations the closing of the anus would not interfere with the production of the froth.

HISTOLOGICAL STUDY OF THE STRUCTURES OF THE GLANDS OF BATELLI

While it is seen that the greater portion of the liquid from which the froth is produced is derived from the anus, there arises the question whether there are not other organs, the secretion of which may take a prominent part in the formation of the spittle.

In the pleural region of the seventh and eighth abdominal somites very large hypodermal glands are located. To the naked eye these glands are not easily discernible upon the nymph, their positions being detected only if there happens to be a large supply of their secretion. Under the hand lens when the abdomen is extended, there are to be noticed whitish patches, even when the secretion

has been completely removed. These, which lie in about the mid-pleural region, are somewhat pulvinate in shape, but by no means regular in outline.

As to the location of these glands there seems to be some difference of opinion. Batelli (1901) describes them as being located on the last two abdominal segments. Misinterpreting Wheeler's (1889) account of the adenopodia of the first abdominal segment in embryos of Nepa and Cicada, he erroneously homologizes these glands of Aphrophora with such structures, but rejects Wheeler's view that they are homologous with abdominal appendages. Porta (1900) and Gruner (1901) believed that these glands are situated on the seventh and eighth abdominal segments, while recently Berlese (1907) gave as his opinion that they were located on the eighth and ninth abdominal somites. I am of the opinion that Porta is correct, for there is no evidence that the first abdominal segment has been suppressed and they are clearly on the existing seventh and eighth abdominal somites (Fig. 2). Moreover, this would harmonize more fully with Ber-

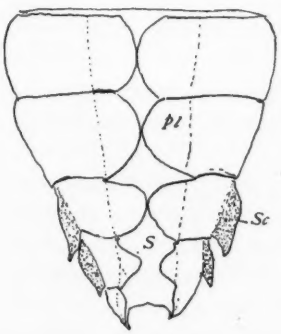

FIG. 1. Ventral View of full-grown Nymph of *L. quadrangularis*, ×40. *Pl*, pleural prolongations; *Sc*, secretion of the glands of Batelli; *g*, groove.

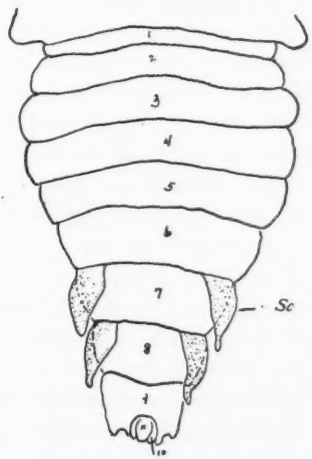

FIG. 2. Dorsal View of younger Nymph of *L. quadrangularis*, ×40. 1-11, tergites; *Sc*, secretion.

lese's own labeling of the segments in the abdomen of *Cicada plebeia* (*Gli Insetti,* Fig. 297, page 263).

An examination of the cuticle in the region of the seventh abdominal gland under the 3 mm. objective of the compound microscope shows that it is free from hairs, which are more or less abundant in other regions of the body. Under the one-sixteenth-inch oil immersion objective one is able to readily discern numerous minute pores (Fig. 3), giving it the appearance of very fine ingrained leather. These pores are more or less regularly distributed over the surface, equally distant from one another, and of equal size throughout the region. Similar pores were found on the eighth abdominal pleura. The most diligent search failed to reveal any such structures in any other region of the body. As I shall emphasize later, these are the openings of true cuticular pores through which the secretions of the underlying glands emerge to the surface.

FIG. 3. Surface View of the cuticular Pores overlying the Glands of Batelli.

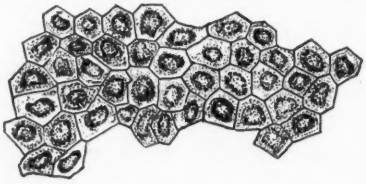

FIG. 4. Surface View of the Epithelium of the Glands of Batelli, × 250.

Specimens of the spittle nymphs were opened and the underlying fat carefully removed. Although it is difficult to separate the fat from this region without destruction of the glands, enough was removed so as to present a satisfactory area for study. The cells (Fig. 4) in good preparations were clearly defined, mostly hexagonal (occasionally pentagonal), though somewhat irregular from mutual pressure. They lie in close apposition to one another. The nuclei are large, round or oval, and in surface view appear situated in the center of the cell.

They are granular and occupy a large portion of the cell. The protoplasm in the region of the nuclei is highly granular and is readily stained. In the periphery of the cell it is not stained as readily, appearing somewhat hyaline. In some of the preparations made with specimens which had been killed in alcohol there were a number of intercellular spaces, while in the preparation of the glands which had been fixed immediately after removal of the fatty tissues such appearance was lacking, except in places where it was obviously due to mechanical cause. Arnhart (1906) gives a photomicrograph of a surface view of the wax-glands of bees, and explains these openings as tracheal in nature. Their presence is, in my opinion, due solely to faulty preparations rather than to the presence of any special tracheal ramifications. In general appearance the cells in surface view are very similar to those of the wax-glands of the honey-bee. A comparison with the excellent figures of Dreyling (1905) serves to bring this out clearly.

In longitudinal sections of *A. parallela* and *Lepyronia quadrangularis* the hypodermal cells of this region are greatly enlarged (Fig. 5), and strikingly resemble those

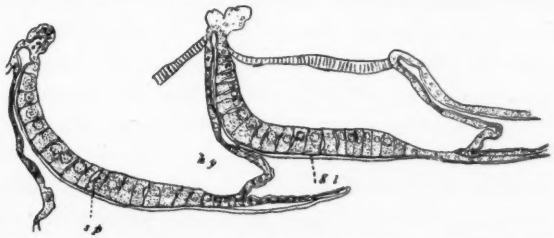

FIG. 5. Frontal Section of the Glands of Batelli in the Nymph of *Lepyronia quadrangularis*, ×125. *Gl*, glandular epithelium; *hy*, ordinary hypodermis of the body-wall; *sp*, spaces.

of the wax-gland of the bees. Each gland has the appearance of a curved band or bow, the central portion of which is thick, while it gradually tapers towards the ends. The same thing is noticed in the cross section (Fig. 6). This appearance is due to the general decrease in height of the

individual cells from the center to the periphery of the glandular mass. The cells in the main body are sharply defined, being separated from one another by distinct lines of demarcation. Near the margin of the gland it is not so easy, however, to define the contour of the individual cells, these passing gradually into the regular type

FIG. 6. Cross section of the seventh Abdominal Segment showing the Glands of Batelli, ×110. *Sg*, sternal groove; *pp*, pleural prolongations.

of hypodermal cells. In this type the nuclei are smaller and the cell outlines are not discernible. In sections of the gland the cells are not uniform in width, due to the fact that the sections pass in the center of some and in the sides of others. The glands of the two segments are about equal in size. In sections that pass through the long axis they are 292 microns in *Lepyronia quadrangularis*, and in *A. parallela* they are 465 microns. Most of the sections which the writer has made show clear spaces (*sp.*, Fig. 5) between the individual cells. These spaces vary in their appearance in different preparations, and evidently represent artifacts due to faulty fixation, rather, than the normal appearance of the cells.

In the middle of the glands the cells are high, cylindrical or cubical. On the margin they are low. In the last instar of the nymphs of *A. parallela* they are 30 microns in height and 18 microns in width in the center

of the gland, while in the margin the measurements are approximately 16 by 14 microns. The nuclei are round or oval and are situated in the lower margin of the cell. They are very granular and stain deeply. They are about 8 by 6 microns in dimensions. The protoplasm is highly granular, much more so in the region of the nuclei and in the margin underneath the chitin. The cuticula over the gland is about 8 microns thick, while that of the adjacent body wall is 12 microns.

If one makes satisfactory sections through the glands of these insects it is very easy to see extremely minute openings in the overlying cuticula leading from the glands to the surface. These outer openings correspond to those described above. For each canal there is a pore. Their distribution over the gland is regular. They are unbranched, perpendicular to the surface of the cells and about equally distant from one another (Fig. 7). As has

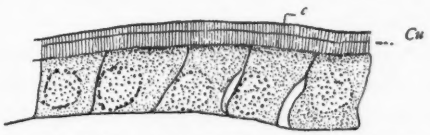

FIG. 7. Enlarged Portion of the Gland of Batelli, showing the cuticular canals, × 275. *Cu*, cuticula; *c*, canals.

been stated, similar pores do not occur in other regions of the body wall. Berlese (1907) and many other writers hold the opinion that true pores are never present in the chitin, and that substances are not conducted through the chitin by any such arrangement. Dreyling (1905), in a paper already referred to, figures and describes canals in the chitin overlying the wax cells of the social bees, and ascribes to these the function of conveying wax to the outer surface. Many writers agree with Dreyling in this view. My studies of the cuticula in the spittle insect convinces me that such true pores are present and they do serve as conduits in carrying the secretions of the underlying glands to the surface. It was noticed on several occasions that in specimens dropped in hot Flem-

ing's fluid the region of the glands was always immediately darkened, while the other parts were not so affected. This was evidently due to a more rapid penetration of the fluid at the point, or the staining of the secretion within the pores.

The above-described glands are also present in the imago, but in this stage they are very greatly reduced in size (Fig. 8) and show many signs of degeneration. The

FIG. 8. Gland of Batelli in adult Insect, ×200. *G*, gland; *h*, ordinary hypodermis.

high cylindrical condition of the cells noted in the nymphal stage is absent, and the sharply defined cell divisions are not present. The protoplasm is scanty and not so granular as in the nymphal stage. Many of the cells show signs of breaking down. Scattered throughout the glandular mass one finds many irregularly shaped bodies which are stained of a pinkish color by the eosin. No spaces were noticed between the individual cells. The nuclei are round and oval and of about the same size noted for the nymph. They show signs of breaking down, in fact some of them are surrounded by clear space, and many had a shrunken appearance.

FUNCTION OF THE GLANDS OF BATELLI

Morse (1900) states that "On the sides of the seventh and eighth abdominal segments may be clearly seen leaf-like appendages, which are possibly branchial in nature." These he figures and describes as "extremely tenuous and having the appearance of clusters of filaments, slightly adhering together and forming lamellate appendages similar to the gill-like appendages seen in the early stages of Potamanthus," though he admits they do not have the definiteness of these structures. Specimens he placed in

water lived for some time and he concludes that the above-referred to structures have a respiratory function. These so-called branchial tufts of Morse (*sc.*, Figs. 1 and 2) are nothing more nor less than the plates of secretion from the glands described above. This secretion is not filamentous, but appears rather very granular. It is very easy to remove these flakes of wax by means of camel's hair brush from the segments to which they adhere but slightly. The secretion is not soluble in alcohol and swells up after being allowed to stand in water for some time. It has a very striking superficial resemblance to beeswax.

The resemblance of these glands to the wax-glands of the honey bee, in the shape of the cells and in the location and appearance of the nuclei is very striking. This fact has already been pointed out by Batelli (1891), Gruner (1901) and others, who also find much in common with the cells of the wax-glands of coccids and other Hemiptera. Gruner (1901) thought that the *wax* served to line the "pocket" already mentioned so as to enable the air to penetrate it the better, and prevent the inflow of the fluid while the bubbles of air were being blown into the fluid. Porta (1900) accepting Morse's curious error regarding the presence of branchiæ, considered this thickened epithelium as a supporting structure for these supposed gills. Carrying further Batelli's misinterpretation of Wheeler's work, he regarded these "supporting structures" as homologous with the abdominal appendages of the embryos of Nepa and Cicada.

I am convinced that these glands secrete a mucilaginous substance which is utilized by the insect in the production of the spittle. Mixed thoroughly with the anal secretions it serves to render this viscid and thus to hold the air bubbles blown into it. This view is based upon the following experiments.

The region of the seventh and eighth abdominal segments of several specimens of the nymph was carefully

seared by means of a heated needle. These specimens were then placed on a plant and, although badly treated by the operation, soon found suitable places and began to suck up the juices, and as usual became enlarged. In the majority of cases each nymph began to emit drops of fluid from the anal opening. Although during the emission of this fluid the caudal segments of the abdomen were extended and retracted as in the normal specimen, in no case were bubbles formed within the secretion. This was true even after twelve to fourteen hours. In order to test whether this was due to the lack of some constituent normally secreted by the injured glands, air was blown into the fluid through a finely pointed tube; instead of being retained, none of the air balls remained in the fluid more than five to ten seconds. On the other hand, bubbles blown into the secretion of unseared specimens held in it for a very long time. This experiment was repeated many times over and always with the same result.

OTHER SUPPOSED SOURCES OF THE SECRETION

Besides these glands, other structures have been mentioned as participating in the formation of the froth, and in order to determine what part they played in it they were given careful consideration.

Berlese (1907) regards the glands of Batelli as the sole source of the secretion. This, my observations, confirming in part those of Morse and others, have shown conclusively to be incorrect. While I hold that the above-mentioned glands contribute an important element to the spittle, there is not the slightest question but that the fluid portion is emitted from the anal opening.

We have seen that Porta (1900) considered the secretion as formed primarily by glands scattered among the hypodermal cells of the abdomen and opening to the surface through prominent canals, and that these were especially abundant in the region of the stigmata. All that could be noticed were the openings of trichopores.

A study of longitudinal and cross sections failed to show any such glands as described and figured by Porta. There are to be found the prominent oenocytes which are more numerous in the ventral surface of the animal. Berlese (1907) dismisses this view by stating that it is these oenocytes which Porta has mistaken for spittle glands. While this is doubtless in part true, I believe, as near as can be judged by the imperfect illustrations, that Porta was also misled by oblique sections through the body wall.

Porta (1900) mentions an oval gland which he says is situated in the fourth somite near the intestine, which he further states is ductless and has no connection whatever with the intestine or any other organ. He thinks that it may be concerned in the formation of the spittle, though he gives no tangible reason in support of this view. After careful study of a number of series of sections I failed to find any such independent gland and I am convinced that he in reality had under observation one of the cephalic glands and that of course it has no relation to the spittle secretion.

This same writer describes other glands which he considers are concerned indirectly in the production of the spittle. These he describes as being situated in the latero-ventral region of the third, fourth, fifth and sixth abdominal segments. He states that there are four pairs of these glandular masses, and in these ramify numerous tracheæ. He was unable to find any external openings to these glands and did not notice their connections with any other organs. The fact is that they are accessory reproductive organs, and that in perfect series their connection with this system may be most readily traced.

Summary

The secretion of the spittle insect is made up from two sources:

The fluid portion is the anal secretion into which the

insect by means of caudal appendages introduces numerous air bubbles.

The glands of Batelli secrete a mucilaginous substance which, added to the anal fluid, renders it viscous and thus causes the retention of the air bubbles.

The so-called branchial appendages of Morse and of Porta are merely plates of this mucilaginous secretion.

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SHORTER ARTICLES AND CORRESPONDENCE

PECULIAR ABNORMAL TEETH IN A JACK-RABBIT

About ten years ago I saw a curious malformation in the skull of a wood-chuck; the upper and lower incisors in some way missed coming in contact with each other in the usual way and had grown up and down through the skull and lower jaw, to wind and twist about above and below completely locking the jaws together. This animal was killed by a hunter near Waverly, N. Y., and is now in the Museum of Cornell University.

Since examining this first one, I have seen and heard of a number of similar malformations and in all cases the teeth of the upper and lower jaws grew more or less irregularly dorsally and ventrally.

A year ago at Claremont, Cal., another peculiar condition was brought to my attention in the skull of a young jack-rabbit (Figs. 1 and 2). In this skull the teeth are most remarkable

FIG. 1. Skull and one half of the lower jaw of a young jack-rabbit with unusual incisors. About half natural size.

FIG. 2. Skull from below and lower jaw from above of a young jack-rabbit with unusual incisors. About half natural size.

in the lower jaw, here the two incisors have grown nearly straight out some distance and are only slightly curved and twisted upon each other. In the upper jaw the incisors are not so long and only twisted at the tips.

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POMONA COLLEGE, CLAREMONT, CAL.
June, 1908.

NOTES AND LITERATURE

ICHTHYOLOGY

Ichthyological Notes.—In the *Proceedings of the United States National Museum,* Volume 33, 1908, Jordan and Richardson give an elaborate review of the Flat-heads and Gurnards of Japan. In a personal letter, Mr. C. T. Regan, of the British Museum, makes one or two corrections in this paper, which may be noted here. The species called *Hoplichthys langsdorfii* by Jordan and Richardson is, according to Mr. Regan, a distinct species, not identical with the original *langsdorfii* of C. and V. The species called *Hoplichthys langsdorfii* by Jordan and Richardson may therefore receive a new name, "*Hoplichthys regani* Jordan and Richardson." The species called *Lepidotrigla microptera* is, according to Mr. Regan, distinct from the original type of that species, which is from Shanghai. The Japanese species should, therefore, stand as *Lepidotrigla strauchi* Steindachner.

In the same *Proceedings,* the same authors give an account of a small collection of fishes from the Province of Echigo, in northwestern Japan, obtained by a local naturalist, Masao Nakamura. Besides the three new species in this paper, the present writer has since received from Mr. Nakamura two other species never before taken in Japan, and which may be recorded here. These are *Podothecus sturioides* Guichenot, and *Dasycottus setiger* Bean.

In the same *Proceedings,* Eigenmann and Bean describe a collection of fishes from the Amazon River obtained by Professor J. B. Steere.

In the same *Proceedings* Mr. B. A. Bean discusses the forgotten genus *Ctenolucius,* a pike-like characin from Colombia.

In the same *Proceedings* Professor John O. Snyder describes a new sucker from the Santa Ana River, at Riverside, California, under the name of *Pantosteus Santa Anæ.*

In the *Smithsonian Miscellaneous Collections,* Volume 48, Mr. Barton A. Bean gives the history of the whale shark, *Rhinodon typicus.* The proper date of this genus is 1829.

In the *Smithsonian Miscellaneous Collections,* Volume 52,

Jordan and Branner give an elaborate account of the fossil fishes of the cretaceous beds of Ceará, Brazil, these specimens being obtained from the Serra do Araripe, the locality from which specimens had previously been obtained by Spix, by Agassiz and by collectors for the British Museum. These specimens are found in concretions of fine clay, and some of them are found to be beautifully preserved when these concretions are opened. In one species, *Calamopleurus cylindricus,* the black pigment at the base of each scale forming stripes along the side of the body is perfectly preserved, and the eye-ball is also well shown. In this collection Jordan and Branner find eleven different species, including all of those described by Agassiz, and including three new genera, Tharrhias, Enneles and Cearana. Most of the species belong to the family of Elopidæ, which represents one of the earlier types of bony fishes.

In the *Occasional Papers of the Boston Society of Natural History,* Volume 7, 1908, Mr. William C. Kendall gives a very useful list of the fishes of New England, and the localities from which each species has been recorded. The list contains 341 species, a number of these being estrays from the south brought northward by the Gulf Stream.

In the *Memoirs of the Carnegie Museum,* Volume 4, 1908, Jordan and Snyder describe and figure three new carangoid fishes from Formosa. One of these, *Ulua richardsoni,* constitutes a distinct genus, separated from Caranx by the extraordinary development of the gill-rakers, which cause the mouth to appear as if "full of feathers," much as in the genus of mackerels called Rastrelliger.

In the *Journal of the College of Science of the Imperial University of Tokyo,* Volume 23, 1908, Mr. Shigeho Tanaka gives a list of sixteen species new to the fauna of Japan, all but one of them new to science. Among these species is the new genus, *Owstonia,* of the family of Opisthognathidæ. Most remarkable of the discoveries is the addition of two more new species of Chimæra to the Japanese fauna. This makes eight species of Chimæra in all, described from Japan, all of them discovered since the year 1900.

In the *Annotationes Zoologicæ Japonenses,* Volume 6, 1908, Mr. Tanaka describes the fishes, sixty-three in number, collected by Professor Ijima in Sakhalin. Of the fauna of this region—

that of northern Japan—two new species, both of Porocottus, are described and figured.

In the *Proceedings* of the Academy of Natural Science of Philadelphia, Volume 59, 1908, Mr. Henry W. Fowler describes a collection of fishes from Melbourne. Among these is a new Chimæra, *Hydrolagus waitei,* for which a new subgenus, Psychichthys, is proposed. In the course of the paper a number of new subgenera are added to the already long list of genera of doubtful value.

In the same *Proceedings* Mr. Fowler has a catalogue of the lancelets and lampreys contained in the collection of the Academy of Sciences. A new genus and species, *Oceanomyzon wilsoni,* is described from the open Atlantic. *Lampetra æpytera* (Abbott) is said to be identical with *Lampetra wilderi,* the common black lamprey of Cayuga Lake. The name *Lampetra æpytera* has priority.

In the same *Proceedings* for 1906 Mr. Fowler describes new and little-known percoid fishes. He uses the name Dules in place of Kuhlia, and describes a new subgenus, Boulengerina, for *Kuhlia malo,* this group being based on the numerous gill-rakers. Some changes of nomenclature are made, based on the adoption of the rule that the first species mentioned in any genus shall become the type. This rule, which would have been just if it could have been originated earlier, will not be accepted by naturalists, as the International Congress has taken the view that in case a type is not fixed by the original author the writer following has a right to fix it, and once established it shall not be changed for any reason. The subgenus Astrapogon is suggested for *Apogonichthys stellatus,* characterized by the very long ventrals.

In the same *Proceedings* Mr. Fowler discusses the heterognathous fishes in the museum at Philadelphia, with descriptions and figures of many of these. Several new species are described, and a number of new generic and subgeneric names suggested.

These papers are subjected to critical review in the AMERICAN NATURALIST, Volume 41, by Dr. C. H. Eigenmann. Dr. Eigenmann claims that many of the new names proposed by Mr. Fowler are quite unnecessary. He says:

> We must feel grateful to Dr. Fowler for his labor. But it is to be

hoped that in the future he will be more conservative in adding names to the science of ichthyology. The valid names do not compensate for the work imposed on some one else to separate them from the synonyms.

In the same *Proceedings* for 1907 Mr. Fowler catalogues the serranoid fishes in the collection at Philadelphia. He substitutes the name "Serranus" for "Epinephelus," for reasons that would be hardly valid even if we adopted the first-species rule, as Cuvier states that his name Serranus comes from the French name Serran, and that the species on which it is based are common in the Mediterranean. In other words, his actual type, although not the species first mentioned, by name, is *Serranus cabrilla*. The subgeneric Chrysoperca is introduced for *Morone interrupta*.

Serranus phœostigmœus is a species of *Epinephelus* described as new from Hawaii. A new species of *Alphestes* is described as *Epinephelus lightfooti* from San Domingo.

Eudulus is proposed as a new name for the genus Dules, which Mr. Fowler regards as preoccupied by Dulus, a genus of birds. Mr. Fowler shows that the number of the "Règne Animal," referring to these fishes, is prior in date to that number of the "Histoire Naturelle des Poissons" referring to the same species. Mr. Fowler also finds that the name malo of Valenciennes is older than that of mato given to the same fish—perhaps by typographical error.

The subgeneric name Callidulus is proposed for Centropristis or *Eudulus subligarius*.

In the *Annals of the Carnegie Museum*, Dr. Carl H. Eigenmann records a large collection of fishes from Paraguay. In all, two hundred and fifty-four species are known from that river basin. Ninety-five of these are peculiar to the Paraguay. One hundred and thirty-two are found also in the Amazon. The amazingly rich fish fauna of tropical America comprises one tenth of all known fishes.

In the *Proceedings of the Washington Academy of Sciences*, Volume 8, 1907, Dr. Eigemann describes a collection of fishes from Buenos Aires obtained by Professor W. B. Scott.

In the *Proceedings of the Field Columbian Museum*, Volume 7, 1907, Dr. S. E. Meek gives notes on fresh-water fishes obtained by him and others from Mexico and Central America. *Cichlasoma milleri* is described as new from Guatemala, and also *Rhamdia regani, Platypœcilus tropicus* and *Pœcilia tenuis*.

In the same *Proceedings*, Volume 7, 1908, Dr. Meek gives an interesting account of the "Zoology of the Lakes of Guatemala."

In *Science*, Volume 27, 1908, Professor J. O. Snyder discusses the region of the fauna of the Russian River in California, showing that these fishes were derived from the Sacramento River by a process of stream-robbing, by which through erosion the Russian River Valley incorporated small streams from tributaries of Clear Lake, which drains into the Sacramento.

In the *Bulletin of Agriculture of the Dutch East Indies*, Volume 8, 1907, Dr. P. N. van Kampen describes two of the mackerel found on the coast of Java. These descriptions are useful, but the synonmy given perhaps needs verification. These mackerel apparently belong to the genus Rastrelliger, distinguished from Scomber by the very great number of gill-rakers, recently described by Jordan and Starks.

In the *Annuaire of the Museum of Sciences of St. Petersburg*, Volume 12, 1907, Dr. L. Berg describes the grayling of Siberia, with a comparative account of their relation to other salmoninæ. The species known as *Brachymystax obtusirostris* from Siberia is made the type of a new genus, Salmothymus, differing from Brachymystax in having the vomer prolonged, with two rows of teeth, as in Salmo. The subgenus Thymalloides is proposed for *Thymallus arcticus*, this group species including also all the American grayling, the name Thymallus being restricted to *T. thymallus*, the grayling of Europe, which does not occur to the eastward of the Ural Mountains. Three species of Hucho are recognized, *H. hucho* in the Danube, *H. taimen* in Siberia and *H. perryi* in Japan. The genus Phylogephyra is recognized for *Thymallus brevirostris*, or *altaica*, of Siberia. This is distinguished by the larger mouth and larger and more numerous teeth, which are present on the head of the vomer and on the tongue.

Dr. Theodor von Kawraysky has published an elaborate account in Russian and in German of the sturgeons of the Caucasus, with lists of other fishes taken in the same region.

In the *Memoirs of the Museum of Comparative Zoology of Harvard* Dr. Charles H. Gilbert gives an account of the lantern fishes collected by the *Albatross* in the South Seas. The species obtained are carefully described, and their synonymy very fully worked out. Several new species are contained in the collection.

The genus Zalarges of Jordan and Williams is identified with Vinciguerria.

In the *Bulletin of the Museum of Comparative Zoology* for February, 1908, Mr. Samuel Garman describes a number of new sharks and skates. The genus Aëtomylæus is proposed for *Myliobatis maculatus*. *Raia kincaidii* is described as new from Friday Harbor, Puget Sound, and *Chimæra barbouri* from Aomori, Japan.

In the *University of Colorado Studies*, Volume 5, No. 3, Professor T. D. A. Cockerell gives a list of the fishes of the Rocky Mountains, with useful notes on geographical distribution, and references to the fossil as well as to the living forms recorded from that region. Brief keys are given, enabling local students to identify specimens in hand.

In the *Zoologischen Anzeiger*, Volume 32, 1908, Dr. Franz and Dr. Stechow describe an interesting case of symbiosis between the fish, *Minous adamsii*, a form of scorpion-fish, and the hydroid polyp Podocoryne from Sagami.

In the *Sitzungsberichte of the Academy of Vienna* for 1908 Dr. Steindachner describes two new fishes from Brazil.

In the *Transactions of the Wisconsin Academy of Sciences*, Volume 16, 1908, George Wagner gives a useful list of the fishes of Lake Pepin, forty-four species being recorded.

In the *Natuurkundig Tijdschrift of the Dutch East Indies*, Volume 67, 1908, Dr. P. N. van Kampen has an interesting series of notes on the spear fishes found in Java. The common species he identifies as *Tetrapturus brevirostris*. *T. mazara* of Japan may be the same species.

In the *Bulletin of the Société Nationale d'Acclimatation of France* Dr. Pellegrin gives a review of the fresh-water fishes of Madagascar, with discussions of the economic value of each species.

Among the papers left at the death of Professor Karl Ernst von Baer is a biography of Cuvier which had never been published, and which is exceedingly interesting as a contemporary account of one of the greatest of naturalists and written by one of his ablest contemporaries. It is published in the *Annales des Sciences Naturelles*, in Paris, by Professor Ludwig Stieda, of Königsberg.

In the *Archivos do Museu Nacional of Brazil*, Volume 4, 1907. Dr. Alipio de Miranda Ribeiro continues his catalogue of the

fishes of Brazil, this volume treating of the sharks, with descriptions of each species, and analytical keys. The memoir is beautifully printed and illustrated by photographs of very many of the species. The synonymy is given in an appendix, and the nomenclature is in general in accord with the rules adopted by American naturalists and by the International Congress.

Dr. C. T. Regan continues the catalogue of the fishes of Central America. *Brycon guatemalensis* is described as new from Guatemala. *Tetragonopterus macrophthalmus* is described from southern Mexico, as is also *T. angustifrons*. Mr. Regan recognizes a number of additional species of Lepidosteus. It is very desirable that the garpikes of the United States should receive a critical review. It is quite possible that more species really exist than the three which have been recognized by Jordan and Evermann. Mr. Regan proposes the name Conorhynchichthys in place of Conorhynchus, the latter name being preoccupied. This paper completes the study of the fishes in the fauna of Central America. It is a very important and very well executed piece of systematic work.

In the *Transactions of the Linnean Society of London*, Mr. Regan gives an elaborate account of the fishes collected by the Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner. One hundred and eighty-five species were obtained, many of them new to science, these being figured in the present volume. Among other interesting forms are six new species of the genus Champsodon.

Under the head of "Edible Fishes of New South Wales," Mr. David G. Stead, naturalist of the Board of Fisheries at Sydney, gives a popular account of the fishes which appear in the markets of Sydney, illustrated by numerous photographs. This interesting and valuable report is accompanied by a map of the state of New South Wales.

Under the title of "Trout Fishing in New South Wales," Mr. Charles Thackeray, of Sydney, gives an account of the various streams in the state, in which trout from Europe and the United States have been introduced. The little volume is extremely valuable to Australian anglers, and is also interesting as showing the remarkable success which has attended the introduction of the California rainbow trout in the Antipodes.

Under the head of "Guide to the Gallery of Fishes in the Department of Zoology of the British Museum (Natural His-

tory)," the trustees of the British Museum have published a book of two hundred and nine pages giving an account of the principal kinds of fishes, the characteristics of the different families, and in general an outline of the classification adopted in the distribution of the species in the museum. A number of figures are given, some of living and some of extinct species.

In the *Transactions of the Royal Society of Canada* Dr. J. F. Whiteaves continues his account of the fossil fishes of the Devonian Rocks of Canada, with descriptions of numerous species and restoration of others. Most interesting is the extraordinary *Bothriolepis canadensis,* restored in accordance with investigations of Professor Patten. This form has many characteristics of arthropod animals. With its head, eyes and coat of mail, suggesting something like a horseshoe crab, it is hard to believe that it is a fish. On the other hand, it is hard to believe that the tail, provided with what seems to be a rayed dorsal fin, can belong to any kind of crab-like animal.

In the *Sitzungsberichte of the Academy at Vienna,* Volume 116, 1907, Dr. Viktor Pietschmann describes two new sharks from Sagami Bay, Japan, *Centrophorus steindachneri* and *Etmopterus frontimaculatus.*

In the same journal for 1908 Dr. Steindachner describes fishes from South America and also a loach from Formosa, the latter called *Homaloptera formosanum.*

In the same journal, Dr. Steindachner describes a new genus of characins called "Joinvillea."

In the same journal he describes also other species of South American river fishes.

In the *Annals and Magazine of Natural History,* 1908, Mr. Regan describes new fresh-water fishes from Japan and Formosa.

In the same journal Mr. Regan describes also new fresh-water fishes from New Guinea.

In the *Proceedings of the Zoological Society of London* Mr. Regan describes a number of new species from Corea.

In the *Annals of the Natal Government Museum* Mr. Regan gives a list of marine fishes from South Africa, nine of them being described as new. Mr. Regan gives also a useful analysis of the eight species recognized by him in the genus Squatina. Of these *S. japonica* and *nebulosa* are found in Japan, and *S. californica* off the coast of California.

In the *Annals and Magazine of Natural History,* 1908, Mr.

Regan gives a synopsis of the sharks, Scylliorhinidæ. To Scylliorhinus are referred the species of Catulus, Cephaloscyllium and Halælurus. The genus Parmaturus is regarded as identical with Pristiurus.

In the same journal, Mr. Regan has a review of the sharks of the family of Squalidæ. In this the name Spinax is preferred to Etmopterus, because of the inaccuracy of Rafinesque's description. *Frontimaculatus* of Japan is regarded as identical with the European *E. pusillus*. The genus Zameus is regarded as identical with Scymnodon. Deania and Lepidorhinus are placed in synonymy with Centrophorus. *Deania eglantina* from Japan is regarded as identical with the European *Centrophorus calceus*. The name Scymnorhinus is preferred to Dalatias, because of the very inaccurate description of the genus of Rafinesque.

In the same journal Mr. Regan describes new loricaroid fishes from South America.

In the same journal Mr. Regan gives a synopsis of the cestraciont sharks. He regards the name Heterodontus as preoccupied by Heterodon, thus accepting the latter name Cestracion. He accepts the genus Gyropleurodus as distinct from Heterodontus.

In the same journal Mr. Regan describes *Cichlosoma lauræ* as a new species from Tampico. *Enneanectes carminalis* was found at Swan Island, near Honduras—a little blenny hitherto known only from Mazatlan.

In the same journal Mr. Regan describes a hybrid between the bream and the rudd, with notes on other hybrids among the European cyprinoid fishes.

In the *Proceedings of the United States National Museum* for 1908, Jordan and Dickerson give an account of fishes obtained by Dr. Jordan at Fiji. The fauna of the islands is essentially like that of Samoa, the physical nature of the reefs being closely identical in the two regions; but even in this small collection are several species which are distinctively characteristic of the New Guinea waters. The deep-bodied mackerel of the Pacific are separated from Scomber to form a new genus, Rastrelliger, differing especially in the very long gill-rakers, the mouth looking as if "full of feathers." With this are other characteristics, the teeth being very minute and there being none on the roof

of the mouth, and there are certain peculiarities in the structure of the bones connecting with the tongue.

In the "Actes de la Société Linnéenne de Bordeaux," 1907, Dr. Pellegrin describes a collection of fishes taken on the west coast of Africa, with useful notes as to their distribution. The nomenclature adopted is rather outworn, and not much notice is taken of questions of priority of names. The illustrations are photographs, very obscurely printed. It may be noted that *Sardinella aurita,* type of the genus Sardinella, is a large-scaled herring of the group called Harengula. The name Sardinella has priority over Harengula, and the name Sardinia must be used for the true sardine.

In the *Comptes rendus* of the French Association for the Advancement of Science, Dr. Pellegrin gives an interesting account of the incubation of the eggs of marine cat-fishes. The male takes care of the egg and the young, taking into the mouth from ten to twenty eggs. The young are retained in the mouth until the yolksac is absorbed. During this period of incubation the male does not feed.

In the *Annals of the New York Academy of Sciences,* Dr. R. W. Tower discusses the production of sound in sciænoid and other fishes. In this very lucid paper it is shown that these fishes "known as drums, croakers or roncadores" have specific drumming muscles, superficially attached to the swim-bladder. For this muscle Dr. Tower proposes the name *musculus sonificus.* The cause of the drumming or grunting noise is the contraction of this muscle, which produces a vibration of the abdominal walls and organs, especially the swim-bladder. In the sciænoid fish, the mechanism is adapted to the production of rapidly repeated sounds or rolls. In other fishes which grunt, as the sea-robin and toadfish, the muscles are intrinsically connected with the swim-bladder, and are known as intrinsic muscles. These muscles produce a vibration in the walls of the swim-bladder which may be repeated at intervals. Dr. Tower gives a number of valuable plates showing the structure of these organs, and also a graphic record of the sounds produced.

In the *Proceedings of the Biological Society of Washington,* H. Walton Clark describes the Plankton of the Lakes of Guatemala.

In the *Bulletin of the American Museum of Natural History,* Volume 25, Dr. L. Hussakof gives a catalogue of the fossil fishes

contained in the American Museum, with figures of many of the fragments.

In the *Biological Bulletin*, Volume 13, Mr. Fernandus Payne describes the effect of light on the blind fish of the Mammoth Cave. In this species the fishes turn away from the light. The young are more sensitive than the adult. The young deprived of eyes are as sensitive as those which have them. They seem to be equally sensitive on all parts of the body, and more sensitive to intense light. They seek the dark without regard to the direction of the rays.

In the Bureau of Fisheries, document 622, Mr. Irving A. Field discusses unutilized fishes, and methods by which these waste species can be rendered of economic service.

In the *American Journal of Anatomy*, Mr. William F. Allen describes the blood-vessels in the tail of the garpike, this paper being a continuation of his series of studies of the circulatory system in different fishes.

In the *Procedings of the American Academy of Arts and Sciences*, Dr. G. H. Parker describes the sensory reactions of the lancelet. This creature possesses in potentia the sense organs of the vertebrate. It is simple in structure, containing forerunners of the lateral-line organs, the ear, the temperature organs, and doubtless the forerunners of the rod- and cone-cells of the vertebrate retina. It is only slightly sensitive to light, but is sensitive to temperature and to sound.

In the *Journal of Experimental Zoology*, Mr. H. H. Newman describes the relation of the hybrids of *Fundulus majalis* with *Fundulus heteroclitus* to problems in heredity. The writer thinks that the study of development and heredity are identical, except that the latter is comparative. No two organisms start out from identical germ cells, nor do they ever develop under identical conditions. Instead of a fixity of relationship between pure strains and hybrids, there is constant flux.

In the *Proceedings of the United States National Museum*, Volume 33, for 1907, Seale and Bean describe the fishes collected in the Philippines by Major Mearns, with seven new species.

In the *Smithsonian Miscellaneous Contributions*, V, 1908, Mr. W. C. Kendall shows that the unrecognized species of whitefish from Saskatchewan River called *Coregonus angusticeps* by Valenciennes is the chub, *Platygobio gracilis*.

In the same *Contributions*, Dr. Jordan shows the identity of

the fossil stickleback from Nevada, *Gasterosteus leptosomus* Hay, with *Merriamella doryssa*. The species stands as *Gasterosteus doryssus*.

In the same *Contributions*, Dr. Gill gives an account of the habits of the miller's thumbs or blobs. He shows that *Uranidea* can not be maintained as a genus distinct from *Cottus* and that the common species must be called *Cottus richardsoni*, not *C. ictalops*.

In the *Transactions of the Wisconsin Academy of Science*, Mr. R. H. Johnson discusses the variations in number and size of the pylone cæca in Sun-fishes. In each species a variation of two or three was found. Thus in species as the rock bass, having on the average eight cæca, the number ranges from six to nine. In the calico bass, with nine, the number ranges from eight to eleven.

DAVID STARR JORDAN.

THE INHERITANCE OF SEX IN HIGHER PLANTS

Digest of Professor C. Correns's Memoir[1]—It is stated in the preface that there is given here a more detailed reiteration of a report made September 18, 1907, to the united sections for zoology and botany of the German Naturalists in Dresden. Experiments in cross-breeding closely related species of plants of different sexual type, carried on since 1900, led to such remarkable results that an account was long withheld. When a repetition of experiments yielded like results, and a reconsideration of the deductions made revealed no flaws, conclusions were announced. For the plants examined the results are regarded decisive; but their wider application must be ascertained by further investigation.

Correns refrains from an historical review of the literature and attempts merely to present some new facts and relate them to previous facts. He does not wish, nor does he claim to be able, to construct a new theory regarding the nature of sex. He believes that there is much in common between his results and those reported by E. B. Wilson for Hemiptera. Finally he explains that by "anlage" of an organ as used in his paper he does

[1] "Die Bestimmung und Vererbung des Geschlechtes nach neuen Versuchen mit hoheren Pflanzen." Abstract presented before a recent meeting of the Medico-Biological Journal Club of the University of Virginia, by H. E. Jordan, adjunct professor of anatomy.

not mean the earliest visible developmental stage, but the representative of the organ in the germ-plasm.

In the introduction Correns notes that the present opinions concerning sex-determination are built largely upon the results (chiefly negative) obtained from attempts to control or alter sex, and upon observations on parthenogenetically developing eggs; in part also upon morphological and statistical data. The main object of his paper is to describe attempts to discover by experimental methods, whether the germ-cells have from the beginning a fixed sex-tendency and if so of what kind, and what rôle fertilization plays in sex-determination. He regards these as fundamental questions which must be answered before one can judge intelligently of the effects of unusual external influences. For the elucidation of these same questions he believes we are largely limited to the plants, particularly the flowering plants, due to the more favorable material they offer for experimentation.

In essence, the fertilization process in plants and animals is the same: two germ-cells unite to form a new organism. Botanists are to-day convinced of the polyphyletic origin of plants and, while it is possible, it is not very probable that sex-determination and sex-inheritance were arrived at in the different groups by the same path of differentiation. A question to be settled by further work, therefore, is whether the principles determined for the particular flowering plants under consideration apply also to other groups of plants, and also to animals.

Already in mosses are found a sharply expressed differentiation of germ-cells into egg-cells and sperm-cells, and this specialization is retained with various slight modifications throughout all the higher groups. In phylogenetically lower forms than the mosses the gametes are all alike (swarm spores). Chance or chemotactic influences may bring such into contact and subsequent union, or they may germinate asexually as in Protosiphon according to Klebs. Externally all are alike. Sometimes, as observed by Klebs in Chlorocytrium, cells from the same mother-cell may copulate. The question arises whether they are intrinsically alike or whether they consist of two classes, + and —, as Blakeslee proposes. In the first case every gamete may copulate with any other and there is sexuality but no sex-differentiation. In the second case only + and — gametes can copulate and sex-differentiation obtains, the foundation for further dif-

ferentiation into egg and sperm not now externally visible. Further development may proceed along different paths. Differentiation may arise between individuals, + and — gametes being then localized in separate members, and the gametes of these same plants may be mutually incapable of union so that only gametes of different plants can copulate. These are here + and — individuals, but the gametes may give no external evidence of a difference. This is the case in Dasycladus according to Berthold and in Ulothrix according to Dodel. Or there may arise differences between the gametes, the one becoming, by the surrender of motility and the assumption of nutritive functions, an egg cell; the other, remaining small and retaining motility, becoming a spermatozoon. Thus hidden differences between + and — germ-cells become conspicuous and there appear "female" gametes and "male" gametes. When the specialized gametes are combined in the same plant it becomes hermaphrodite or monoecious; when separted, dioecious forms appear.

Correns lays emphasis on several points: (1) That the differentiation of gametes into egg and sperm has nothing to do with the union of the two germ-cells for the production of a new individual; or, in other words, that the externally visible differences between egg and sperm need have no connection with the process of fertilization; (2) individuals may be differentiated into males and females without an evident external mark of differentiation either in the individuals themselves or in their germ-cells. The various differential characters of eggs and sperm-cells and all other visible differences between male and female individuals reveal only their different nature, but do not touch the essence of sex itself. Interesting confirmatory observations in this connection are those of Blakeslee on Mucorineæ.

Originally there is present only the "determination" in the germ-cells which renders possible the union of some pairs of germ-cells and prevents the union of other pairs. All else is of a secondary character. With few exceptions the higher animals are unisexual. Among the higher plants many different sexual types occur. Neglecting transition conditions, the main types are hermaphrodite forms where stamens and pistils are united in the same flower; bisexual or monoecious forms, where pistils and stamens are separated into female and male flowers; unisexual or dioecious forms, where the male and female flowers

are borne by different individuals. By far the larger majority of flowering plants have hermaphrodite flowers. Separation of sexual organs on different flowers or different individuals appears here and there as characteristic of entire families, and relatively often as a specific character, or sometimes only as a variation; and this in the most distantly related groups.

Correns entertains no doubt that hermaphroditism is the primary type and dioeciousness the derived. He does not regard as conclusive the arguments advanced by Coulter and Chamberlain that it is impossible to decide which is the primary condition since dioeciousness appears in both the quite low and the higher groups of flowering plants, being related in the former to wind-pollination and in the latter connected with insect-pollination. He observes that sex-separation appears also in other groups without any relation to the high or low degree of other characters. The dioecious condition arises in consequence of the physiological or morphological disappearance of one or the other set of members of the hermaphrodite condition. The "degeneration" of a sexual organ here is really nothing else than an arrest at a certain stage in the development of one or the other element in the hermaphrodite flower (Hofmeister; Goebel), thus producing the monoecious or dioecious conditions. Such change naturally does not proceed without an alteration of the idioplasm of the species involved; the "anlagen complex" of one element must become more or less incapable of development, or latent. As far as we know this process follows independently in both sexes and, in each, internal and external alterations stand in intimate correlation. Male and female flowers of monoecious species are of like high development. The female is not a male arrested at a lower stage of development. The great differences in size and vitality between germ-cells must be regarded as adaptations.

The main points involved in the problem of this investigation concern the *method by which* sex is determined and the *time when* such determination takes place. Since the embryonic and the adult sex-organs contain the anlagen for the characters of both sexes, sex-determination has to do with the question as to which anlage, male or female, shall develop. These conditions demand that the germ-cells have a fixed sex-tendency already before their union at fertilization. Correns emphasizes also that one must not here think of a separation and distribution of

anlagen for the sex-characters into separate germ-cells in the sense that into one animal wander testes-anlagen (determinants of Weismann) and into another ovary-anlagen. This as far as we know is not the case. Both germ-cells carry both sets of sex-characters, as experiments with hybrids abundantly show. That a germ-cell has male or female sex-tendency means only that the male or female anlagen are in condition of capability to develop. As to how one anlage in the germ-cells becomes active and the other is brought to a latent condition we have no positive knowledge.

One may entertain several possibilities respecting the time that sex is determined. He may take the position that the germ-cells have held from the beginning the tendency to develop into one or the other sex—which sex becomes apparent when caused to develop by artificial parthenogenesis—and that the tendency remains unchanged by fertilization; in other words, that the germ-cells are unalterably fixed as to their sex-tendency and thus independently determine the sex of their offspring pure: "progame" determination. Either all the sperm or all the eggs are so determined or only a part of each. Such predestination is commonly ascribed to the egg, and the sperm is thought to be without influence. Accordingly, half the eggs must be male and half female in tendency.

The second position ascribes to the germ-cells before fertilization no fixed tendency to develop into a particular sex, and holds that only at fertilization is the decision made as to what sex the offspring shall have: pure "syngame" determination.

According to the third position the product of the union of the two germ-cells has no fixed sex-tendency. External influences determine only during the later stages of development what the sex of the offspring shall be: pure "epigame" determination. Theoretically an "epigame" alteration of sex must be possible, since the embryo contains both sex-anlagen. All critical investigations, however, both zoological (O. Schultz) and botanical (E. Strasburger), indicate that the means thus far employed in attempting to produce an alteration of sex-tendency have yielded no significant results respecting the actual separation of sex-organs among different individuals. Primarily, attempts must be made to determine whether the germ-cells of unisexual forms have an indifferent sex-tendency or whether they have a fixed tendency. If the latter condition prevails, it

is incumbent next to determine what this tendency is. There are several possibilities: (1) The germ-cells may have the sex-tendency of the plant from which they came, the egg-cells the female, the sperm-cells the male; (2) they may have the opposite sex-tendency; or (3) some of the eggs may be of one sex-tendency and a part of the other, and likewise the sperm. A further problem arises as to how far fertilization plays a rôle in sex-determination, since thus germ-cells of different sex-tendencies may unite; and also how far external influences have significance in that they can act upon the sex-tendency of the germ-cells before fertilization, or at the time of fertilization upon the united product, or after fertilization on the embryo.

Whether a given germ-cell contains a fixed sex-tendency can best be ascertained when such a cell can be caused to develop without fertilization into a sexually mature individual. Such conditions obtain in cases of "habitual parthenogenesis." The facts here at first sight seem to compel acceptance of the position that the sperm-cells play no rôle. However, on closer scrutiny of the facts, doubts are raised as to the validity of such an interpretation. One must not forget that generally eggs that develop parthenogenetically do not undergo a reduction division. Correns states that whatever significance one may attach to reduction, he can not regard such eggs as of like nature with those that have suffered maturation. In the case of "habitual parthenogenesis" one deals with phenomena of adaptation. Such adaptation may enable an egg to develop without fertilization even though this capacity depends only on the suspension of a check, which otherwise, through the intervention of a male germ-cell, could exert its influence. In similar manner the sex-tendency also may be influenced. Natural and artificial parthenogenesis yield an indication of the sex-tendency only of the egg. "Ephebogenetic" development of sperm-cells, theoretically possible, but practically thus far beset with insuperable difficulties, is urgently required. Merogony furnishes no positive results until we know definitely the rôle of cytoplasm, as distinct from karyoplasm, in heredity.

Correns turns into other fields which seem to lead farther than experiments with artificial parthenogenesis, namely, hybridization. The controlling idea of Correns's investigation is the following: The egg-cells of a dicœcious form whose sex-tendency

we desire to ascertain, is commonly fertilized by a sperm-cell of the same species. The sex-tendency of both gametes is unknown. On the other hand, the sex of the offspring resulting from the union of the gametes becomes obvious. In other words by the interaction (in union) of two unknown quantities, X and Y, *i. e.*, the sex-tendencies of the two gametes, there results an organism of known sex; or $x + y =$ sex of organism. Could the value of either x or y be ascertained the equation could be solved and the value of the other unknown quantity determined. These values Correns obtains in the case of the germ-cells of two favorable, nearly related, species of plants one of which is hermaphrodite and the other dicœcious. The above figure is not quite accurate, as Correns point out, since a solution of the equation is possible only when the unknown sex-tendency of the germ-cell of dicœcious type, as over against the known sex-tendency of the hermaphrodite germ-cell, is so strong as to wholly or almost entirely prevent the development of the latter or to greatly suppress it. The conditions are fully met in those cases where the sperm-cell of a white-flowering pea by fertilization makes possible the development of the egg-cell of a red-flowering pea, so that a red-flowering plant results without showing a trace of the white factor of the sperm. Thus is obtained the effect of artificial parthenogenesis, not only on the egg cell but also on the sperm-cell.

The germ-cells of hermaphrodite forms carry the hermaphrodite sex-tendency and give rise only to hermaphrodite forms. Correns does not regard a hermaphrodite individual as a "mosaic" derived from the union of a germ-cell of male tendency with one of female tendency. However, they must contain the anlagen of such a mosaic. Hermaphrodite germ-cells contain only the hermaphrodite sex-tendency both in the egg-cells and in the sperm-cells. Likewise for monœcious forms, where on the same individual two kinds of sexual flowers appear, male and female, the same position must be taken; *i. e.*, that both kinds of germ-cells, eggs and sperm, carry the same tendency, namely, the tendency to develop into monœcious forms. Each germ-cell thus carries over not the sex of the flower from which it came, but that of the entire plant on which the sexual flowers appeared.

There remains no doubt concerning the monœcious tendency of the germ-cells of monœcious plants. Correns cites in further

support of this position the case of *Dimorphotheca pluvialis*, a "trimonœcious" form where flowers of three kinds, male, female and hermaphrodite, occur in the same head. Since we have here two kinds of sperm-cells (pollen), one from the hermaphrodite flower and one from the male flower, and also two kinds of eggs, embryos can arise in four different ways. If the germ-cells had different sex-tendencies after they are built into a male, a hermaphrodite, or a female flower, four kinds of offspring would arise. All the seed, however, produce the same kind of offspring, *i. e.*, trimonœcious forms. Therefore all the germ-cells of Dimorphotheca must bear the tendency again to give origin to trimonœcious plants. It may be said then, that all germ-cells of a hermaphrodite plant have the tendency again to develop into hermaphrodite plants, whether they be found in stamens or pistils. All germ-cells of monœcious forms have the tendency again to produce monœcious forms whether they arise in male or female flowers. We know, then, the tendency of the germ-cells in hermaphrodite and monœcious types and we can employ these known quantities to ascertain by cross-breeding the unknown tendency of the germ-cells of unisexual plants.

In the first three experiments Dr. Correns employed two species of Bryonia, a genus of the Cucurbitaceæ, growing wild in central Europe. *Bryonia alba* bears a black fruit and is monœcious. *Bryonia dioica* bears a red fruit and is dicœcious. In the first experiment (A) he pollinated the pistils (egg-cells) of *Bryonia dioica* with the pollen of *Bryonia alba*. He obtained eleven hybrid offspring from the seed, all female plants and perfectly sterile. These results disclose the following facts: (1) That monœciousness was here recessive to the dicœcious conditions; (2) that the egg-cells of *B. dioica* had before fertilization, "progame," a fixed sex-tendency, and all of the same kind. Were this not the case, not all the offspring could have attained the same sex. Had both anlagen, those of the male and those of the female sex, been equally active in the eggs and had a decision as to the definitive sex depended upon a struggle between the anlagen (or upon external influences), the hybrid offspring would have been of dissimilar sexes; (3) the egg-cell has the tendency to develop into a female plant; also the tendency to give origin to such plants as those from which it arose; the physiological sex-determination and the developmental tendency are both female.

The second experiment (B) consisted in fertilizing the egg-cells of *Bryonia dioica* (using flowers from the same plant as used in Experiment A) with pollen from the same species. Of 67 seedlings in the first year 41 came to flower, 21 being male and 20 female, all pure *B. dioica*. Combining the results of this experiment with those of experiment A it becomes positive that the egg-cell possessed a definite sex-tendency, and that the sex was not, however, unalterably determined in it; otherwise in experiment B all the offspring would have become female as in experiment A. The sperm-cells also must have played a rôle in the sex-determination, since until the time of impregnation of the eggs by the male gametes the conditions of both experiments were the same. As far as this experiment discloses, all the pollen-grains might have carried the male tendency. After union with the egg-cells of female sex-tendency a struggle may be conceived to have proceeded, the victory coming now to the female tendency, and now to the male, so that the final outcome resulted in 50 per cent. individuals with definite male characters and 50 per cent individuals with female characters. That this was not the case, the third experiment (C) makes clear.

In experiment C, female flowers of *Bryonia alba* were pollinated by male flowers of *B. dioica*. In other words, *B. alba* furnished the egg-cells and *B. dioica* the sperm-cells. The fruit of the cross was black, and of 87 seedlings, 76 came to bloom the first year, 38 of which were female and 38 male. All the plants showed hybrid characters and were completely sterile. The decision in regard to the sex of the hybrid must have been brought about through the influence of the male gamete (pollen) as in experiment B, since *B. alba* self-pollinated gives rise only to monœcious plants. There is here a second point in evidence, unconnected with the first, against the unalterable "progame" determination of the egg-cells, and in favor of ascribing definite influence to the sperm-cells and to fertilization. The pollen-grains of *B. dioica* can not all have been alike in regard to sex-tendency, else the offspring would all have been of the same sex, since the egg cells of *B. alba* were all alike in their tendency to give origin to monœcious forms. Again, not all the pollen-grains of *B. dioica* can have had the same sex-tendency, else all hybrids, due to the dominance of diœciousness, would have had the same sex. Nor can they have been endowed merely with the tendency of diœciousness, but without a tendency for a

particular sex. Nor can the sex of the hybrid have been determined by the union alone, else in experiment B, where these male gametes united with female gametes all with fixed sex-tendency (the female tendency as determined in experiment A), all offspring would have been alike female plants. Thus there remains only this interpretation: That half of the pollen-grains of *B. dioica* were endowed with the male tendency and half with the female tendency. Since half of the offspring were male and half female, and all of the eggs were of the same sex-tendency, there can not have occurred a struggle for supremacy between the anlagen of the two tendencies (such a condition would yield 75 per cent. female plants and 25 per cent. male plants) but the male sex-tendency must have dominated completely over the female tendency. Sex-determination is thus "progame" and "syngame"alike, but the decision comes "syngame."

Experiments were repeated with *B. dioica* from widely separated regions. Different plants of *B. alba* were also employed. Dr. Correns has had under observation about 1,000 of these hybrids. In 27 experiments, using 16 female plants of *B. dioica* from various regions and 4 plants of *B. alba,* 589 plants were raised and all were females. In 17 experiments, using 5 plants of *B. alba* from different regions and 10 plants of *B. dioica,* 358 hybrids appeared, 171 pure males and 187 pure females. In the body of his paper Correns discusses numerous possible objections and criticisms that might be made in respect to his experiments and the interpretation he gives to his results. All such objections and criticisms are met with very keen and reasonable explanations.

Correns made a fourth series of experiments (D) in which he used plants from a family of only distant relationship to the Cucurbitaceæ. These were a kind of pink, *Melandrium album,* and a plant from a closely related genus, *Silene viscosa.* The former is a diœcious form and Silene is hermaphrodite. Of the seedlings from this cross, using Melandrium as the female parent and Silene as the male, 27 plants came to bloom. They were all female, though in other respects hybrid in character, and sterile. In another experiment (E) Melandrium was fertilized with pollen from its own species (as in experiment E) and there appeared approximately 50 per cent. male plants and 50 per cent. female. The parallel of experiment C with Bryonia was also attempted between Melandrium and Silene, using the latter

as the female parent (the hermaphrodite flowers were castrated) and Melandrium as the male parent. All the seed from this cross was sterile.

Numerous experiments with phylogenetic transition forms ("polyams") between hermaphrodite and monœcious flowering plants on the one hand and hermaphrodite and dicœcious forms on the other, *i. e.*, andromonœcious, trimonœcious and gynomonœcious forms—also with androdicœcious, tricœcious and gynodicœcious forms—yielded results less definite, it is true, but nevertheless confirmatory (especially as regards the female tendency of the egg-cells of the female plant) of those obtained from hybridization experiments between the end forms as in Bryonia Melandrium and Silene.

The main results may be summarized under three heads: (1) The germ-cells of female individuals all have the tendency to develop into female plants; one half of the germ-cells of the male individuals have the tendency to develop into male plants and one half into female. (2) The definitive sex-determination occurs at fertilization; the original tendency of the female germ-cells can be altered through the sex-tendency of the male germ-cells. (3) When at fertilization germ-cells of unlike sex-tendency unite, the male tendency dominates over the female.

The experiments seem to indicate that sex is inherited. Strictly speaking, however, one can not say that a plant has "inherited" sex, but only that the germ-cells have inherited sex-tendencies. Only the anlagen of sex are transmitted from generation to generation, not the characters ("Merkmale")—the cloak that they have woven for themselves (Naegeli).

Had the hybrids of Bryonia, and those between *Melandrium album* and *Silene viscosa* not been sterile, they would undoubtedly have split up in such a way that the anlage of dicœciousness would have been again separated from that of monœciousness and of hermaphroditism, respectively, and the second generation of these dicœcious hybrids would have included pure dicœcious, hybrid dicœcious and pure monœcious (or hermaphrodite) individuals in the Mendelian proportion of 1:2:1. It remains a question whether the dicœcious plants would all have had the sex of the dicœcious parent or if both male and female plants would have appeared.

In all cases in which the offspring are divided approximately equal in respect to sex, and where the eggs show no external

differentiating characters, as in the great majority of the diœcious Metazoa and man, there appears nothing to contravene the facts and hypotheses regarding sex-determination as presented in the foregoing description of the experiments with certain of the higher flowering plants. However, such cases as are presented by the aphids and the honey-bee, where all fertilized eggs develop into organisms of like sex, are disconcerting from the view-point of the above facts. Correns proposes that the drone eggs of the honey-bee are incapable of fertilization (develop parthenogenetically). He inclines also to the idea that all the eggs may have the male sex-tendency and that femaleness dominates. But since all fertilized eggs develop into females this necessitates, on the hypothesis that there are two kinds of sperm-cells, the further assumption of selective fertilization. The recent discoveries of Meves, Stevens and Morgan, that during spermatogenesis of the honey-bee, certain aphids and phylloxera, respectively, one half of the spermatozoa degenerate (and these probably are the male-producing kind) now brings these cases into very close harmony with Correns's observations on plants. Thus all fertilized eggs must develop into females. The disturbing question still remains as to just how a parthenogenetic female aphid can produce male offspring.

Again when two kinds of eggs are produced, as by phylloxera, daphnids and rotifers, the larger invariably develop (parthenogenetically) into females and the smaller into males. Correns believes that here a proportion of the eggs may have become altered ("umgestimmt") in sex-tendency and that their size-difference stands in correlation with the difference in size of the female and male individuals. In phylloxera this difference, however, does not seem significant. *Dinophilus apatris* seems to be a real exception to the hypothesis that sex is determined by the spermatozoon. Nevertheless, Correns suggests that a portion of the eggs, in consequence of a subsequent alteration or originally, may have retained the male sex tendency; or selective fertilization may obtain, so that only the larger eggs are fertilized by female producing spermatozoa and the smaller by male producing. However, when caused to develop parthenogenetically large and small females appear, the difference in size of the eggs being related to size differences of the offspring and may have arisen through "prospective" adaptation. This argues

for the influence of the spermatozoa in sex-determination and for selective fertilization.

While the facts regarding the honey-bee and Dinophilus offer serious obstacles for the general application of Correns's principles of sex-determination to plants and animals, he finds on the contrary much similarity between his results and the cytological findings of E. B. Wilson for many of the Hemiptera. Taking Protenor and assuming that the spermatozoon with the seven chromosomes (including the accessory) carries the recessive female tendency, and that the spermatozoon with six chromosomes carries the dominant male tendency, then the correspondence between the results is complete. The assumptions made at first sight seem inconsistent, but they appear more reasonable in the light of Correns's observations on *Satureia hortensis* where the female tendency—which becomes patent by reason of the latency of the anlage of the male tendency (in originally hermaphrodite forms)—dominates over the hermaphrodite tendency in crosses, when ordinarily the anlagen for hermaphroditism are active besides the passive anlagen for the female tendency (in gynomœcious forms).

Correns finds it difficult to believe that the idiochromosomes are the material vehicles of the sex-tendency, since the disappearance of the mate of the accessory chromosome in Protenor seems to show directly that it was no sex-determinant. Both germ-cells contribute both anlagen; the idiochromosomes can, therefore, simply aid the development of one sex-anlage or hinder the other. If we accept the idea that they are also the carriers of the sex-anlagen then the spermatozoon of Protenor with six chromosomes would have no sex-anlage; and ephebogenetically developed it would give rise to an organism without sex. If the anlagen are present outside of the idiochromosomes then the spermatozoon thus developed would give origin to a hermaphrodite form. There probably are not two kinds of eggs. The contrary assumption rests upon another; *i. e.*, selective fertilization. There is no experimental evidence of selective fertilization in the case of Hemiptera. If one accepts Wilson's suggestion that in cases like Nezara (where the idiochromosomes are alike) half of the spermatozoa have an active idiochromosome (aiding the development of the female sex) and half a passive one (permitting the male sex to develop), and that the latter may, in consequence of its passivity become reduced (as in

Lygaeus), or have entirely disappeared (as in Protenor), all the eggs may then carry idiochromosomes of like activity and there is no need for selective fertilization. These cases accordingly seem to lend themselves for interpretation very well to the principles above stated for sex-determination in Bryonia. In Mendelian terminology, females are pure zygotes, *i. e.*, homozygotes; males are hybrids, *i. e.*, heterozygotes. Segregation takes place at maturation and produces by the homozygote organism one kinds of germ cells and by the heterozygote two kinds, *i. e.*, male and female in sex-tendency.

The physiological male or female property of the germ-cells which provides for their union and what relates thereto, must not be confounded with the male and female tendency of the germ-cells, or the disposition to give rise to descendants whose germ-cells are again male or female. Though these principles of sex-determination and inheritance discovered for higher plants may not be capable of universal application, there are several points in which the different methods may agree: (1) That each germ-cell has originally a fixed sex-tendency; (2) that the germ-cells of one sex (either the male or the female) have only one and the same sex-tendency, and those of the other partly the one, and partly the other; and (3) that a primarily fixed differentiation in the developmental vigor of the germ cells with different sex-tendencies that unite at fertilization, brings about a decision favorable to one or the other sex.

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